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A 53-YEAR RECORD OF FOREST SUCCESSION FOLLOWING FIRE IN NORTHERN LOWER MICHIGAN

Samuel M. Scheiner and James A. Teeri

Dept. of Biology
University of Chicago
Chicago, Ill., 60637

A 53-year record of forest succession following fire was analyzed for five experimentally or naturally burned plots in northern Michigan. After a fire the species diversity increased gradually for 25 years and remained level thereafter. This finding contrasts with studies which have found an early peak in species diversity with a subsequent decrease within the first 10 years of succession. Immediately following fire, *Populus grandidentata* became the dominant tree species. During the 53-year period *Acer rubrum*, and *Pinus strobus*, replaced *Populus grandidentata* in abundance. In contrast with other investigations, the importance of annual species did not decrease during the period of succession.

The process of successional change in plant communities has been studied in many kinds of habitats. However, most such studies were based on data sets of only a few years' duration. The few analyses of long-term successional patterns have been based on data collected at one time in several sites of similar physiography, but with each site at a different stage of succession. In this way Shafi & Yarranton (1973) analyzed a 44-year sequence in northern Ontario, and Oosting (1942) reconstructed a 200-year sequence in the North Carolina Piedmont. However, these studies have the limitation of being an indirect measure of long-term succession at a single location. In addition, there are many difficulties in locating precisely dated sites that can be ascertained to differ only in the time at which succession began. The present paper is a report of a long-term study of succession following fire in which the dates of the fires are precisely known and the same sites were sampled over a number of years.

Frank C. Gates (1917, 1926, 1930) studied forest succession in the Douglas Lake region of northern Michigan from 1911 to 1954. As part of these studies, from 1923 until 1954 he made yearly surveys of several areas that had experienced fires and also established an experimental area in which he clearcut and burned three adjacent plots of forest, one each in 1936, 1948, and 1954. The purpose of this paper is to analyze 30 years of successional data collected by Gates spanning 53 years of succession following fire. These data, unanalyzed at the time of Gates' death in 1955, remained in the files of the University of Michigan Biological Station. In addition, we resurveyed two of the experimentally burned plots in 1978 and included the data in the analysis. The data set, with a total of 32 sample years, presented a unique opportunity to study succession because the locations and dates of all fires were known precisely. More important, the burned sites remained undisturbed since the time of burning.

Successional data from five burned plots at the Biological Station are considered. According to Gates' records, two of the plots experienced natural

forest fires in 1901 (Plot 1) and 1923 (Plot 2). The three other plots are part of the experimental area established by Gates. In each of these three plots an area of approximately 100,000 square feet, or one hectare, was clearcut and the plant material burned *in situ* in 1936 (Plot 3), 1948 (Plot 4), and 1954 (Plot 5). The data collected by Gates were obtained by his Plant Ecology classes in 1939 and from 1946 through 1954. The data set consists of a listing of all vascular plant species observed in each plot and the frequency index for each species encountered in quadrat sampling of each plot. The frequency index is the percent of the meter-square quadrats in which a particular species occurred in a given plot. Gates sampled between 30 and 100 quadrats per plot each year. We assume that the frequency index included identifiable individuals of all age classes.

In 1978, our survey of plots 4 and 5 followed the above methods which are outlined on Gates' data sheets and cited in Gates (1949). The frequency index for all species in each plot was determined by surveying 100 one meter square quadrats. Five parallel lines were laid five meters apart on a N/S compass heading within the plots, and quadrats were measured at intervals of three meters. All species were recorded in each quadrat. Insofar as possible identifications were updated to accord with nomenclature used by Voss (1972) for gymnosperms and monocots and Fernald (1950) for other taxa. In *Amelanchier* and in the case of *Hieracium paniculatum,* the taxa of old lists could not be ascertained, and so the original designations were retained. We made graphs of the frequency index for the 113 species for the 32 sample years. These graphs are now part of the permanent record of forest succession in the Director's files at the Biological Station. In each of the graphs (e.g., Figs. 2–6), the individual data points are indicated by a number that corresponds to the actual plot number in which the observation was made.

The total list of all 113 species encountered during the 32 sample years is presented in Table 1. The number accompanying each species indicates the year after fire in which that species had the greatest frequency index over the entire 32 sample years. In all of Gates' records the first 23 species listed in Table 1 are called trees and all remaining species are called herbs. We have also used these designations, with the result that some shrubs are referred to as trees.

One measure of succession is change in species diversity through time. The inverse Simpson index which is sensitive to changes in common species (Peet, 1974) was calculated for each sample year. For the purpose of calculating these values, it has been assumed that the frequency index is proportional to density (Gleason, 1920). The proportion (p_i) of species i was then calculated by dividing the frequency index (FI) of species i by the total frequency index for that year summed over all species. The Simpson index (L) is given by the equation:

$$L = \Sigma(p_i)^2, \quad \text{where } p_i = \frac{\text{FI}_i}{\Sigma \text{FI}_i} \quad \text{(Simpson, 1949)}$$

with 1/L being the inverse. This index shows an increase in diversity for the first 25 years and a leveling off thereafter (Fig. 1).

As anticipated, some species (Table 1) reached their greatest frequency soon after fire and thereafter declined in frequency. Both *Populus grandidentata* (Fig. 2) and *Carex rugosperma* (Fig. 3) exemplify this pattern. In contrast, other species which were present in low frequency in the years immediately following fire gradually increased in frequency over the 53-year period. *Acer rubrum* (Fig. 4) and *Pinus strobus* (Fig. 5) are examples of this pattern, as are *Diervilla lonicera, Oryzopsis asperifolia,* and *Pedicularis canadensis.* A few species, such as *Pteridium aquilinum* and *Vaccinium angustifolium* (Table 1), exhibited a relatively unchanging high frequency over the entire 53-year period.

The total number of vascular plant species and the number of tree and herb species counted per sample year are given in Table 2. The column labeled "Plot" in Table 2 indicates which of the five plots provided the data for the corresponding year after fire. The average number of vascular plant species counted per plot was 39 over the 32 sample years. There was a small trend toward an increasing number of species through time (Table 2). The number of tree species reached 16 species per plot in year 16 and thereafter remained fairly stable (Table 2). The number of herb species remained relatively stable at ca. 26 species per plot over the 53-year period.

In Fig. 7 is given the percent contribution of three life forms—trees, annuals and biennials, and non-tree perennials—to the total frequency index for each of the 32 sample years. The percentage for each life form was calculated by summing the frequency indices of all species of a given life form and dividing by the total frequency index summed over all species.

From Table 1 it is evident that there was a wide range of times at which different species attained a peak frequency. However, it appears (Fig. 7) that there was a relatively uniform representation in the percent frequency index of the three life forms over the entire 53-year period. There was, however, a change in the composition of species. During the early years *Populus grandidentata* was the dominant tree (Fig. 2), because extensive suckering from roots, undamaged by clearcutting and burning, makes aspen a fire follower (Graham et al., 1963; Shirley, 1932). As the aspen thinned, it was replaced by *Acer rubrum* (Fig. 4) and *Pinus strobus* (Fig. 5), which were gradually increasing in frequency. *Quercus rubra* and *Betula papyrifera* increased in frequency during the same period.

Several species give evidence of an apparent dissimilarity between the naturally-burned plots (1 and 2) and the experimentally burned plots (3, 4, and 5). There is a step-wise increase in the frequency index of these species, such as *Maianthemum canadense* (Fig. 6), comparing all the data for naturally-burned and experimentally-burned sites. There are two years (24 and 30) for which data exist for both naturally and experimentally burned plots, and the difference also appears in these years (Fig. 6). Plots 1 and 2 are located near the shore of Douglas Lake and presumably have moister substrates. In contrast plots 3, 4, and 5 are located at the top of a gravel ridge and appear to have considerably drier soils. We have not attempted to quantify differences in microhabitat between natural and experimentally burned plots. However, these differences deserve study as they may be great enough to modify the successional process.

TABLE 1. All vascular plant species observed in the 5 sample plots (over a period of 53 years) and the year after fire at which each species had its greatest frequency index.

Acer rubrum	53	Gaylussacia baccata	24
A. pensylvanicum	29	Gnaphalium macounii	10
A. saccharum	2	Habenaria orbiculata	28
Amelanchier canadensis	24,47,53	Hepatica americana	46
A. huronensis	30	Hieracium aurantiacum	24
A. spicata	46,49	H. florentinum	24
Betula papyrifera	48,50	H. paniculatum	53
Cornus rugosa	46,52	H. scabrum	24
Fagus grandifolia	23	H. venosum	3
Fraxinus americana	53	Hypericum perforatum	30,46
Pinus banksiana	24	Krigia virginica	11
P. resinosa	3	Lactuca canadensis	26
P. strobus	51	Lepidium virginicum	10
Populus balsamifera	–	Linnaea borealis	24,52
P. grandidentata	1	Lonicera canadensis	48
P. tremuloides	4	L. dioica	46
Prunus pensylvanica	52	Lycopodium tristachyum	25
Quercus rubra	3,30,31,46,	Maianthemum canadense	29
	50	Medeola virginiana	25
Rhus typhina	3,51	Melampyrum lineare	31
Salix humilis	23,30,45	Mitchella repens	25,47,48
Thuja occidentalis	–	Monotropa hypopithys	29,30,31
Viburnum acerifolium	53	Comptonia peregrina	3
V. cassinoides	52	Nemopanthus mucronata	49,50
Agrostis gigantea	10,11	Oenothera biennis	10
Anaphalis margaritacea	4,6	O. parviflora	11
Antennaria neglecta	30	Oryzopsis asperifolia	52
A. neodioica	51	O. pungens	24
Apocynum androsaemifolium	16,38,45,50	Panicum columbianum	24
Arabis glabra	6	P. depauperatum	4,6
Aralia nudicaulis	31	P. xanthophysum	3,4,53
Arctostaphylos uva-ursi	31	Pedicularis canadensis	25
Asclepias syriaca	1,5	Poa compressa	12
Aster laevis	25	P. palustris	23
A. macrophyllus	3,46	P. pratensis	10,11
Carex communis	2	Polygala paucifolia	52
C. lucorum	3	Polygonatum pubescens	16
C. rugosperma	6	Pteridium aquilinum	1,2,3,6,12,
Chimaphila umbellata	30		24,25,27,
Clintonia borealis	52		46–49,51
Comandra umbellata	16	Pyrola elliptica	25
Convolvulus spithamaeus	24	P. secunda	24
Cornus canadensis	50	Rhus radicans	38,51
Corallorhiza trifida	51	Rosa sp.	48,49
Cypripedium acaule	53	Rubus allegheniensis	38
Danthonia spicata	6	R. canadensis	–
Diervilla lonicera	46,47	Rumex acetosella	3
Epigaea repens	53	Senecio pauperculus	27
Epilobium angustifolium	46	Silene antirrhina	1,4
Erigeron annuus	5,6	Smilacina racemosa	45
E. canadensis	3	S. stellata	28
E. strigosus	11	Solidago canadensis	24
Festuca ovina	24	S. hispida	24
Fragaria virginiana	24,26,53	S. juncea	6
Gaultheria procumbens	27	S. nemoralis	–

TABLE 1. Continued

Taraxacum officinale	53	Vaccinium angustifolium	4,53
Trientalis borealis	29	V. myrtilloides	27
Trifolium repens	50	Verbascum thapsus	10
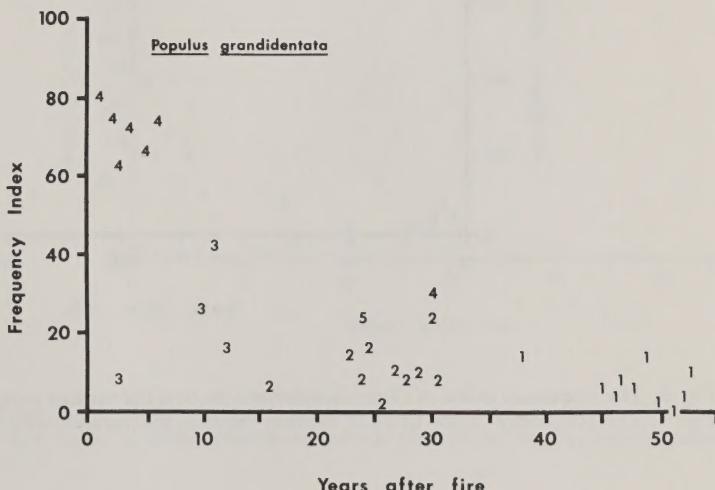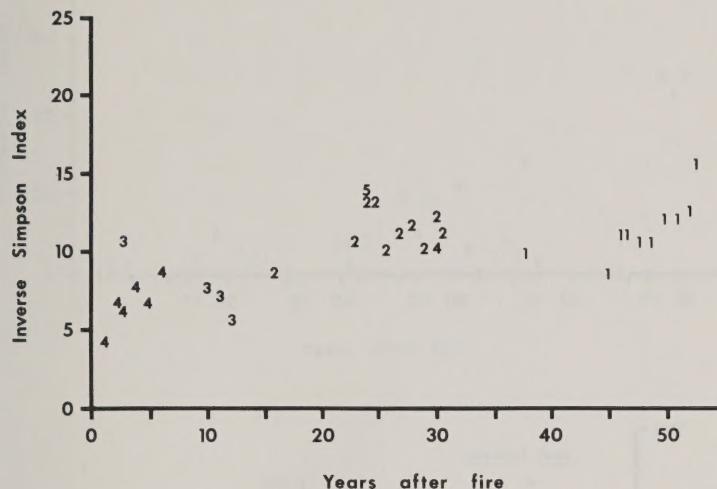
Fig. 1. The Inverse Simpson Index plotted for various sample years after fire. The data points are given as numerals that correspond to the plot number in which the data were obtained for a particular sample year. Fig. 2. The frequency index of *Populus grandidentata* plotted for various sample years after fire.
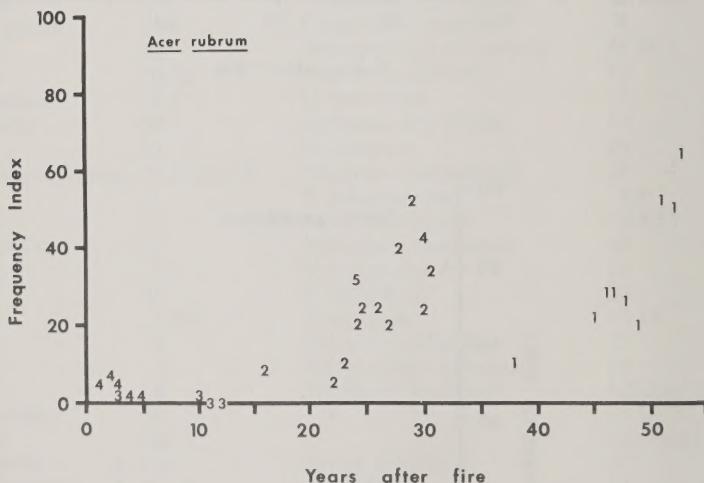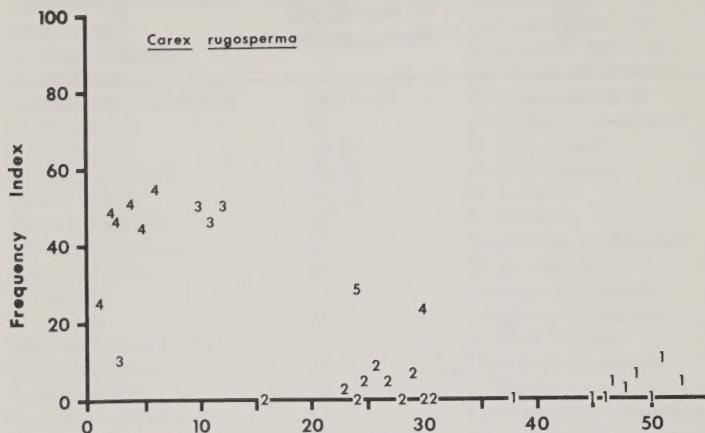
Fig. 3. The frequency index of *Carex rugosperma* plotted for various sample years after fire.
Fig. 4. The frequency index of *Acer rubrum* plotted for various sample years after fire.
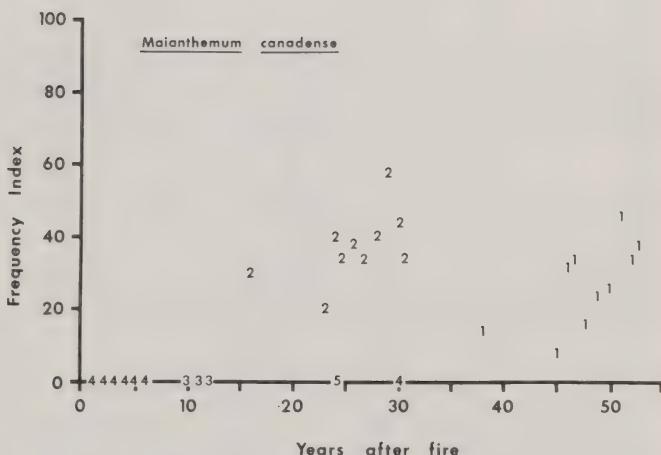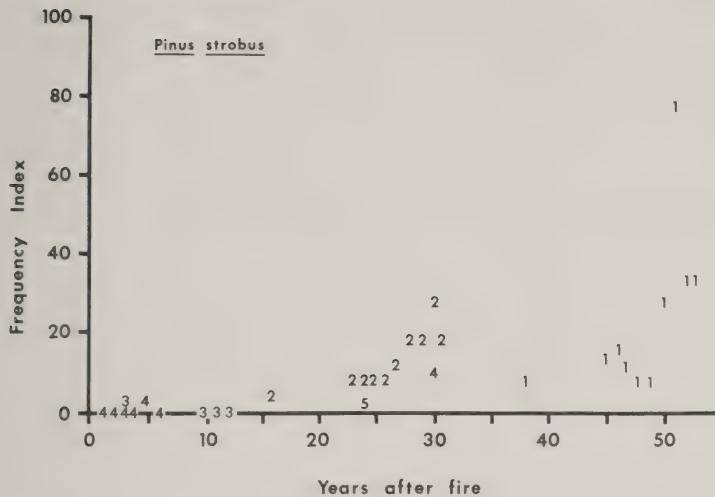
Fig. 5. The frequency index of *Pinus strobus* plotted for various sample years after fire.
Fig. 6. The frequency index of *Maianthemum canadense* plotted for various sample years after fire.

TABLE 2. The number of species, tree species, and "herb" species per plot at intervals over 53 years following fire.

| Year after Fire	Plot	Number of Species	Number of Tree Species	Number of Herb Species
1	4	33	8	25
2	4	35	9	26
3	3	43	12	31
3	4	34	8	26
4	4	32	7	25
5	4	36	9	27
6	4	45	10	35
10	3	33	10	23
11	3	34	11	23
12	3	31	12	19
16	2	44	16	28
23	2	34	12	22
24	2	45	16	29
24	5	33	11	22
25	2	47	14	33
26	2	45	16	29
27	2	42	13	29
28	2	44	18	26
29	2	34	14	20
30	2	35	12	23
30	4	30	11	19
31	2	31	12	19
38	1	45	16	29
45	1	39	14	25
46	1	50	16	34
47	1	43	16	27
48	1	48	18	30
49	1	40	16	24
50	1	42	16	26
51	1	43	15	28
52	1	38	14	24
53	1	43	14	29

DISCUSSION

As noted above, there are significant differences in species composition between natural and experimental plots. Some of these may be due to the successional process. The available data from the experimental plots comes mainly from the first few years after fire. The natural burns cover the later years. The problem is to separate out which differences are temporal (i.e., due to succession) and which can be attributed to physical environmental variables. There are only two years (24 and 30) with data from both natural and experimental burns, and therefore analysis of differences between these sites must be constrained. The most noticeable differences are in composition of the understory. Although several species show a step-wise change in their frequency between the two areas, this is not true of most species. The relationships between
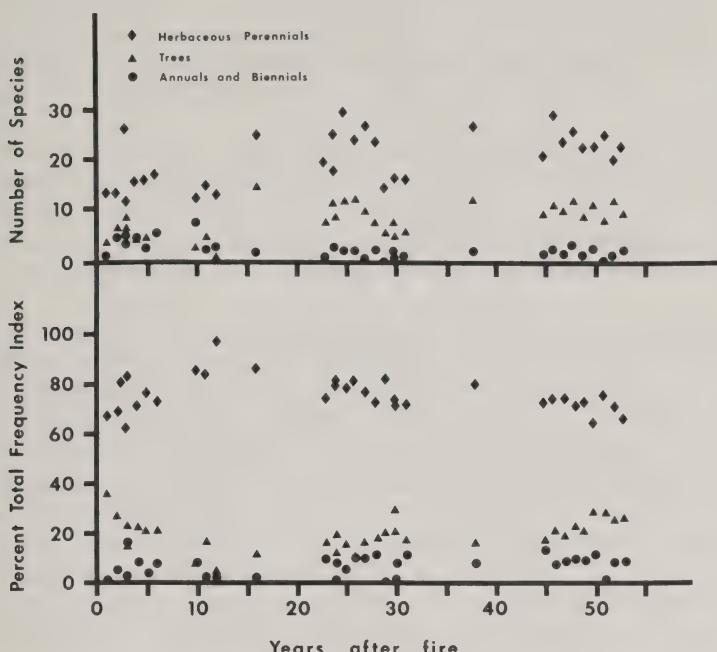
Fig. 7. Upper: The total number of tree species, annual and biennial species, and herbaceous perennial species at various sample intervals over a 53-year period following fire. Lower: The percent of the total frequency index that is constituted by tree species, annual and biennial species, and herbaceous perennial species over a 53-year period following fire.

microhabitat differences and correlated differences in succession clearly deserve further study.

For year 3 duplicate surveys are available for plots 3 and 4. As those plots are contiguous and differences due to the sites are thereby minimized, they may give some indication as to the variance in the data. Caution must be exercised, however, because of having only two data points to compare. Comparison of plots 3 and 4 in that year reveals large differences in values of the Simpson index, total number of species (Table 2), and some individual species frequencies. Often these differences are greater than those between the values for years 24 and 30. This may mean that variance inherent within the successional process is greater than that due to microsite differences. However, large variances may be inherent only during the first few years. This would seem likely if succession has a significant stochastic component. It might be expected that the variance would decrease through time. If so, it would not be possible to say whether the variance seen in years 24 and 30 is within the expected limits.

There is a further problem with the original data that is due to the variation in the number of quadrats counted in plots 1 and 2 by Gates. A regression of the number of quadrats sampled versus the number of species found gives a

significant positive correlation (r=.724, p<.01, d.f.=17). There is also a significant positive correlation between the number of quadrats counted and the frequency index of a given species (Gleason, 1920). Therefore, it is not possible to ascertain how much of the variation seen from year to year is due to sampling error.

Despite these cautions there do seem to be consistent patterns in the data. The inverse Simpson index points for the duplicate years of plots 4 and 5 fall within the range of those from plot 2 (Fig. 1). Additionally, the trees do not show the same intersite differences that understory species do. It may be that trees as a group are less sensitive to minor environmental differences than herbs.

Given the above cautions, some conclusions as to the course of succession can be made. There is a smooth increase in the diversity of the forest for the first 25 years with a corresponding increase in the density of plants in these sites. This smooth pattern of increase in species diversity differs from that in many previous studies which have described an early peak in diversity. Dayton (1975), in a study of old field succession, found a peak after one year. Williams et al. (1969) found a peak after a year and a half in a clearcut and burn study of a subtropical rainforest. In studies of North American boreal forests, both Auclair & Goff (1971) and Shafi & Yarranton (1973) discovered a similar early peak. In the latter the peak came at eight years. According to Horn (1974), this phenomenon is caused by the overlapping of early and late successional species. Although clearly such overlapping is occurring in the present case, there is no clear division between early and late successional species.

Beckwith (1954), Dayton (1975), and Horn (1974) all proposed an orderly succession of annual and biennial species being replaced by perennials. A pattern of decrease similar to Beckwith's is seen in the number of annual species. However, their importance, as indicated by the proportion of individuals (Fig. 7), does not decrease but increases slightly. This is caused primarily by an increase in the frequency of *Melampyrum lineare* (Table 1), a root parasite dependent on the presence of any of several tree species, including *Pinus* spp. and *Populus* spp., for normal growth and reproduction (Cantlon et al., 1963). Thus the increase of *M. lineare* during the development of the forest is not surprising. The analysis, however, does agree with the description (Horn, 1976) of succession of the northern temperate forest in that most of the species and nearly all of the tree species are present from the beginning of the successional sequence.

The pattern of succession seen here is similar to that previously reported for comparable forests. Graham et al. (1963) and Whitford (1901), in studies in northern Michigan, indicate a procession of aspen and birch leading to pine and finally a beech-maple-oak forest. Both Stallard (1929) and Skutch (1929), in studies in Minnesota and Maine, reported similar sequences of aspen and birch during the first years after fire. Gates (1930), in earlier investigations, stated that the pines should begin to displace the aspen in 30 to 40 years. Lorimer (1977), in a study in Maine, found that the birch-aspen dominance apparently lasted a minimum of 75 years after fire. Graham et al. (1963) concurred with this view. The present findings support those of Gates. Within the 53-year

period, *Pinus strobus* and *Acer rubrum* have already replaced *Populus grandidentata* as the dominant forest trees. Gates (1926) reported that *Pinus strobus* and *P. resinosa* formed the presettlement climax forest in the study area. He mentioned (1930) *Acer rubrum* as a secondary species and listed *A. saccharum* as a relic of the original forest. Graham et al. (1963) noted that *A. rubrum* is an invader in this area. Possibly the devastation of the forest has permitted the introduction of *A. rubrum* leading to a change in the climax forest of this area.

One species, *Epilobium angustifolium* (Table 1), is conspicuous by its absence during the first years after fire. Its common name of fireweed reveals its status as a classic fire follower. The absence, especially surprising as the species is recorded by Gates (1930) as frequent the first two years after fire elsewhere in the Douglas Lake area, may indicate the importance of the composition of the surrounding forest on the course of succession. The area which was clearcut and burned is small, and it is surrounded by forest which was at least 30 years old at the time. The surrounding forest may have been a sufficient barrier to dispersal to prevent *E. angustifolium* from colonizing. An alternative explanation may be that the soils in the study sites were too depleted in nitrogen to support a vigorous growth of *E. angustifolium,* as suggested by Summerhayes & Williams (1926) in England.

In the same way, the youth of the forest would have an effect on the suckering of aspen. There would still be an extensive system of roots at the time of burning. It is known that the number of suckers per unit area is proportional to the number of trees present before burning (Graham et al., 1973). Therefore, the course of succession following fire in the present forest may be very different from that in the primeval woodland or immediately after its destruction.

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SEED DISPERSAL IN WILD CARROT (DAUCUS CAROTA)

Elizabeth P. Lacey

Dept. of Biology,
University of North Carolina,
Greensboro, 27412

While animals and wind have been proposed as agents of seed dispersal for *Daucus carota,* a common weed, no quantitative data can be found in the literature to support either. This paper presents evidence to support both modes of dispersal. Seeds attach to fur coarser than that of rabbit, and also disperse by wind. Spines appear to facilitate both mechanisms. Wind can disperse seeds locally and over long distances and is probably the more frequent dispersal agent.

In spite of the importance of seed dispersal to weedy plants, little information about dispersal vectors is available for *Daucus carota,* a common species of abandoned fields and other disturbed habitats. Evidence for dispersal by animals comes from seeds that have been germinated from excreta of roe deer (Ridley, 1930) and found in horse dung (Salisbury, 1961) and nests of wrens (Ridley, 1930); however, the number of such observations is unknown. Also, *D. carota* seeds make up 0.5–2% of the diet of Ruffed Grouse, Ring-necked Pheasant, Pine Mice, and Cotton Rats in the northeastern United States and 2–5% of the diet of the Townsend Mole in Washington and Oregon (Martin et al., 1951). Most evidence for animal dispersal comes from observations on fruit morphology. Stebbins (1971) stated that *Daucus* has evolved a fruit with hooks and spines that aid in dispersal by animals, and Salisbury (1961) indicated that because of curved spines on the ribs of the fruit, the seeds of *D. carota* are often spread by animals. The implication is that seeds are unintentionally transported on animal fur and on clothing, although no data support this conjecture. Dale (1974) reported that, in addition to animal dispersal, seeds can be blown for short distances by wind, or long distances over crusty snow, but again no supporting evidence was given. This paper presents observations on fruit morphology and experiments designed to test the efficacy of wind and animals as dispersal agents for *D. carota.*

Daucus carota, commonly called Queen Anne's Lace or Wild Carrot, has spread across the continent in northern United States and southern Canada and as far south as the Georgia Piedmont in the eastern United States since its introduction from Europe. North American populations and some European populations belong to the informal group "subspecies aggregate" *carota* (Small, 1978).

In southeastern Michigan, *D. carota* disperses fruits from late August through the winter. The fruits, which are borne on compound umbels (Fig. 1), usually split into two one-seeded mericarps which disperse separately. The mericarp separates from the carpophore, first in the middle and subsequently from either the base or the tip. (Because each mericarp contains one seed, I will, for simplicity, refer to seed dispersal rather than mericarp dispersal.) Four rows of large spines project from a mericarp, and one to several barbs may be found at the tip of each spine. The number of barbs per spine may vary from one to
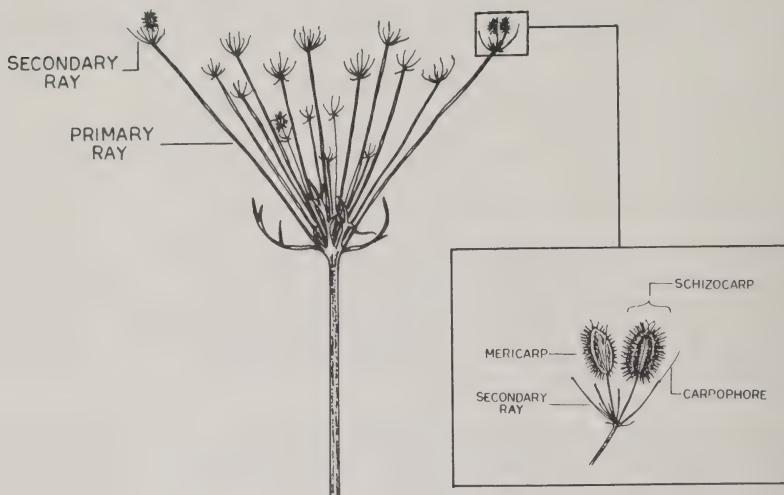
Fig. 1. A compound umbel. (A mericarp is one half of a schizocarp.)

five (Fig. 2–5), and associated with the number of spines is a characteristic angle. The mean angle formed by the barbs and spine is ≤90° for spines with four or five barbs (Fig. 2 & 3). The mean angle for spines with two or three barbs is ∿90° (Fig. 4) and for spines with one barb ≥90° (Fig. 1). Although plants that I sampled have predominantly one barb per spine, the number varies among individual plants (Table 1). That found in 15 European specimens I examined is lower than the 3–5 barbs per spine reported by Heywood & Dakshini (1971) for European populations.

　　The presence of barbs, especially more than one per spine, and the presence of spines on mericarps suggest that seeds might be dispersed by animals. To examine the effectiveness of animal dispersal, I dropped seeds onto the fur of live field and meadow mice (*Peromyscus leucopus, P. maniculatus,* and *Microtus* sp.) and a raccoon and also onto prepared skins of badger, skunk, and rabbit to see how well the seeds would stick. Seeds did not stick to the rabbit or mice fur because of the fine and thin nature of the fur. Seeds lodged in the coarse hair of the raccoon, badger, and skunk and could be removed only by deliberately picking them up.

　　An alternative hypothesis about the function of spines and barbs is that they decrease the rate of fall of seeds through air and that seeds are dispersed by wind. To examine this possibility, I conducted experiments to compare dispersal distances of seeds that were intact, barbless, or spineless. To compare intact and spineless seeds, I selected 60 seeds whose spines appeared to the naked eye to be present and in good condition. The seeds were divided without regard to size or shape into two samples of 30 seeds. One sample was rubbed between the hands to remove all spines, and the other sample was left intact. Independently, I placed each sample on a piece of cardboard directly in front of
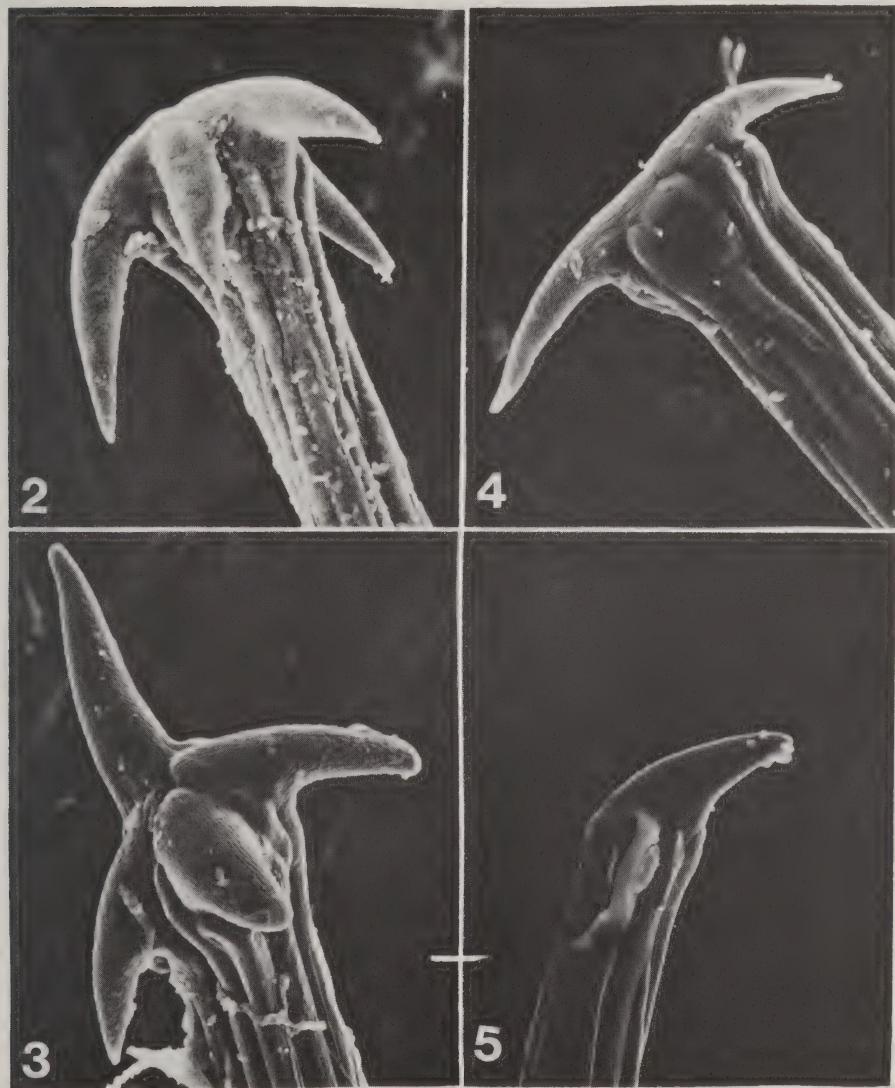
Fig. 2–5. Examples of barb number and orientation on spines of *Daucus carota* seeds. 2–3. Mean angle of barbs ≤90° for 4 or more barbs per spine, ×768 and ×664, respectively. 4. Mean angle of barbs ∿90° for 2–3 barbs per spine, ×676. 5. Mean angle of barb ≥90° for one barb per spine, ×569.

TABLE 1. Variation in barb number per spine in individuals of *D. carota* from North America and Europe.

	Barbs per Spine			
	1 barb >66%	1−2 barbs >66%	3−5 barbs >66%	intermediate number or highly variable
North America				
United States (Calif., Wis., Mich., N.C.)	12*	8	1	4
Canada (N.S., N.B., Que., Ont., B.C.)	16	2	3	3
Europe				
(France, Belgium, Denmark, Romania, Sweden, Portugal, Italy, Germany)	6	0	2	7

*number of individual plants

a window fan on the floor. I held the cardboard 0.42 m above the floor and initially protected the seeds from the force of the wind (with a velocity of 4 mph) by holding vertically a second piece of cardboard between the seeds and the fan. When I removed the vertical piece of cardboard, the seeds dispersed onto the cheesecloth spread on the floor in front of the fan. I then recorded the distance from each seed to the fan. This experiment was replicated three times. On the average, spineless seeds (mean distance = 0.33 m) went only two-thirds as far as the intact seeds (mean distance = 0.45 m), even though the spineless seeds weighed less (mean weight of intact seeds = 1.12 mg; mean weight of spineless seeds = 1.01 mg). A Kolmogorov-Smirnov test (Siegel, 1956) indicated that the difference in distribution was highly significant ($D = 0.36$, $p < .001$).

To compare intact with barbless seeds, I selected 22 seeds whose spines and barbs appeared to be intact when viewed under a dissecting microscope at high power. Only seeds that had many spines with three or more barbs were chosen. I measured the dispersal distance for the intact seeds in the same manner as in the previous experiment. I then soaked the seeds in water for a few minutes to soften the spines and thus to reduce the damage while removing the barbs. Using the dissecting microscope and scissors I cut off the barbs; although I tried to minimize spine loss, in most cases a bit of spine was removed as well. After letting the seeds dry, I remeasured the dispersal distance. The intact seeds (mean distance = 0.53 m) went slightly farther than the barbless seeds (mean distance = 0.49 m). A Mann-Whitney U-Test (Siegel, 1956) indicated that the difference was just barely significant ($Z = 1.68$, $p = .0465$).

To examine wind dispersal under natural conditions, I conducted outdoor experiments in fall and winter. Information on fall dispersal comes from two experiments in which seeds dispersed from isolated plants stuck in the ground which was covered with blankets and cheesecloth to catch the seeds (Lacey, 1978). Mean distances were 2.06 m and 2.43 m, and no seed was found farther than 6.25 m from the plant even though the material on which the seeds were caught extended at least one meter beyond the farthest seed collected. During the time of dispersal the mean wind speed was 6–7 mph with gusts to 16 mph as measured by a continuously recording anemometer. In fall 1975 I constructed a cage of chickenwire (1.52 × 1.53 × 1.52 m) and set it over several carrot plants to observe seed disappearance in an environment where mammals larger than mice were excluded. (These plants were growing on the George Reserve where a deer population is maintained.) The small number of plants prevented the collection of quantitative data; however, plants inside and outside the cage appeared to lose seeds at a similar rate.

I gathered information about dispersal in winter over snow on three windy days by laying seeds on the snow to observe how far they moved over the surface. I observed seeds moving over both crusty and powdery snow when the wind exceeded 12 mph. On a day of winds 15–25 mph I laid cheesecloth (3.66 × 0.91 m) against an upright fence bordering a softball field and released 300 seeds sixteen meters upwind. All seeds disappeared from my hand as soon as I released them, and 37 were collected in the cheesecloth. Because of shifting winds the other seeds probably were blown out of the range of the cheesecloth and consequently traveled much farther.

Morphological and experimental evidence thus indicates that *D. carota* seeds may be dispersed by wind and on animals. Seeds can be transported on the coat of mammals with fur coarser than that of rabbits. I have also transported seeds myself on wool clothing and occasionally in cuffs of jeans. The spines and barbs undoubtedly facilitate this dispersal. However, spines also aid in wind dispersal by decreasing the rate of fall of seeds in air. The barbs have little effect, if any, on this fall rate. The fact that intact seeds dispersed only slightly farther than barbless seeds might be attributed to the removal of spine material when the barbs were removed.

An aspect of dispersal that is often overlooked is that there may be selection not for just one mode of dispersal but for several modes of dispersal particularly in environments where presence of any one vector may be unpredictable. For example, morphological structures may evolve that facilitate several types of dispersal. The dual role of spines in *D. carota* illustrates this point.

Any conclusions drawn from this study regarding the relative importance of animals and wind as dispersal agents are speculative. Quantitative data on patterns of animal movement through old fields, grooming behavior, and abundance of animal dispersers are lacking. Animals most often encountered in the eight fields where I collected demographic data in 1976 and 1977 were rabbits, deer, and mice; I also saw two badger mounds. Mice and rabbits do not have fur coarse enough to retain seeds for dispersal. No doubt badgers, deer, dogs, and humans pick up seeds; however, the seed number is probably minuscule in proportion to the millions of seeds produced in one carrot population. While I

could pick up a few dozen seeds by walking through a dense patch of carrots, one plant can produce from several hundred to more than 15,000 seeds (Lacey, 1978). The few trails that appeared to be made by animals (such as deer) skirted rather than penetrated the dense patches of carrots, which become tough and scratchy on dying. These observations suggest that while animals do disperse seeds, wind is probably the more frequent vector. This is further supported by the absence of differences in seed disappearance from caged and uncaged plants.

Forces favoring a particular dispersal mechanism in *D. carota* may not be the same over its entire range especially because of its recent expansion into North America. Reported evidence for animal dispersal appears to come from observations of European plants; while animal dispersal may be most important in Europe, wind dispersal may be more important on this continent. If this is true, one would predict an eventual decrease in barb number per spine in American populations; my data are consistent with this possibility, though the European sample size is small. It will be interesting to see if in the future dispersal behavior of North American populations diverges from that of European populations.

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GYPSOPHILA MURALIS — IS IT NATURALIZED IN MICHIGAN?

Richard K. Rabeler

Dept. of Botany & Plant Pathology
Michigan State University
East Lansing, 48824

Plants introduced either by intention or accident often create problems for anyone compiling information on the local flora. Reference manuals may not list them, and herbarium collections may be sparse or misidentified. Some species form perpetuating populations, at which time, the species is said to be naturalized at that site (Daubenmire, 1978). Several members of the Caryophyllaceae, among them *Gypsophila muralis* L., have been introduced into Michigan. This account will attempt to clarify the history and distribution of this species in Michigan.

As described by Barkoudah (1962), *G. muralis* (Fig. 1) is a shallow-rooted annual, 5 to 20 cm (to 40 cm in Barkoudah & Chater, 1964) tall, with small, linear leaves and a spreading, much-branched inflorescence. The flowers have a ciliate-margined calyx and pink or white petals that are less than 1 cm in length. Seeds develop in an oblong capsule and are small (0.5 × 0.5 mm), dark, and snail-shaped. Several common names have been applied to this species—Mist, Low Gypsophila, Cushion Gypsophila (Dole, 1937), and Cushion Baby's Breath (Swink, 1974).

According to Barkoudah (1962), *G. muralis* is the only member of the genus considered to be "ruderal," that is, growing in disturbed areas. It is one of the most widely distributed species of the genus, apparently radiating outward from western Turkey, where its nearest relatives occur. The shape of the calyx, position of the stigma, and shape of the capsule resemble typical character states of the genus *Saponaria,* causing some concern that *G. muralis* should be transferred to *Saponaria.* Barkoudah (1962) cited small seeds similar to those of other species of *Gypsophila,* hyaline bands between adjacent calyx teeth, and a lax, dichasial cyme inflorescence as reasons for retaining it in *Gypsophila.*

In Table 1, *G. muralis* is compared with *G. paniculata* L., Baby's Breath, a large and often-cultivated perennial naturalized in the northern Lower Peninsula of Michigan (see Pringle, 1976, for other introduced *Gypsophila* species), and *Petrorhagia saxifraga* (L.) Link [*Tunica saxifraga* (L.) Scop.], Tunic Flower or Coat Flower (Schlising & Iltis, 1962), an introduced perennial now locally common in a few areas of the Lower Peninsula. The latter bears a strong resemblance to *G. muralis* and has been mistaken for it by some collectors. The two can be distinguished by the absence (*G. muralis*) or presence (*P. saxifraga*) of bracts subtending the calyx. This character cannot be used to separate all species of *Gypsophila* and *Petrorhagia,* since about one-half of the species of *Petrorhagia* lack these bracts. Ball & Heywood (1964) noted that the seed offers the only constant characters by which the genera may be separated.

During the course of this study, specimens of *G. muralis* from 13 states, all in the Northeast and Great Lakes regions, and two Canadian provinces were

Fig. 1. *Gypsophila muralis.* Collection made by E. J. Hill at Montague, Mich., in 1899.

TABLE 1. *Gypsophila muralis* compared with two related species found in Michigan, taken from Barkoudah, 1962, and Ball & Heywood, 1964.

	G. muralis	*G. paniculata*	*Petrorhagia saxifraga*
Habit	annual	perennial	perennial
Stem			
height	5–40 cm	40–100 cm	5–45 cm
pubescence	scabrous below	± scabrous below	scabrous below
Leaf			
length	1–2.5 cm	2–5 cm	0.5–2.5 cm
shape	linear	lanceolate	linear
base	ciliate	not ciliate	ciliate
"epicalyx" bracts	0	0	4, partially surround calyx
Calyx			
length	2.5–4 mm	1.5–2 mm	3–6(–7) mm
lobe margin	ciliate	not ciliate	ciliate
Petals			
color	pink or white; dark pink veins	usually white; no dark veins	white or pink; dark pink veins
Style	stigmatic along entire style	stigmatic along upper 1/3 of style	stigmatic along entire style
Seed			
length	0.5 mm	1.0 mm	0.9–1.6 mm
width	0.5 mm	1.0 mm	0.6–1.1 mm
embryo	peripheral (curved)	peripheral (curved)	central (straight)
tubercles	flat	obtuse	flat
shape	snail-shaped	snail-shaped	pear-shaped
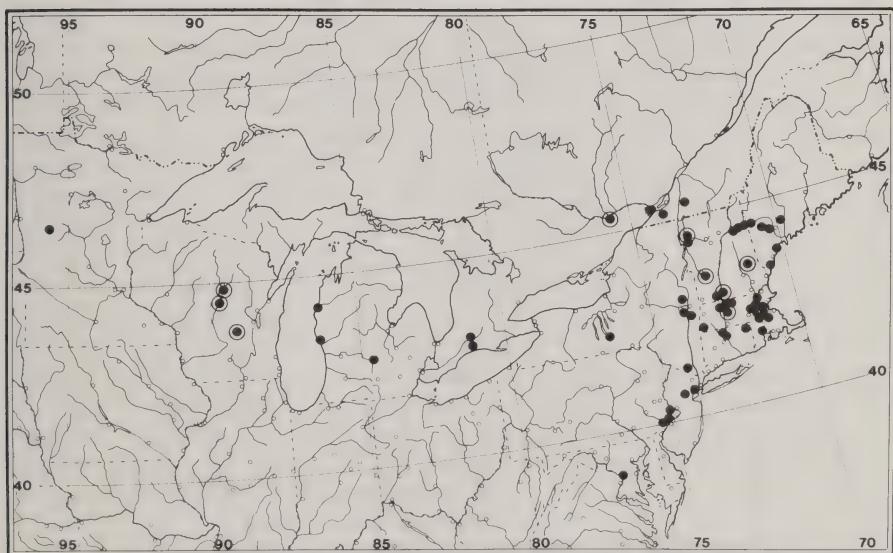
Fig. 2. North American distribution of *Gypsophila muralis* based on herbarium specimens. Circled dots represent post-1960 collections.

examined (see Fig. 2); various authors have cited *G. muralis* in Illinois (Pepoon, 1927), Indiana (Hull, 1938; Swink, 1974), and South Dakota (Van Bruggen, 1976). A review of this information indicates that *G. muralis* has been introduced both as a desired cultivated plant and an unintentional "visitor." The earliest record of the species in North America is a collection from Philadelphia, probably from the ballast grounds of the Navy Yard (*Fiot* in 1866, PH). Other early locations include Nassau (Rensselaer Co.), New York (*Wibbe* in 1873, NA; see Anon., 1876); Cambridge Botanic Garden, Massachusetts (*Martindale* in 1877, NA); the wharf near Communipaw Ferry, New Jersey (*Brown* in 1879, GH, NA, NY); and London, Ontario (*Dearness* in 1887, GH). A large number of collections bear dates between 1885 and 1920, with the number dropping considerably after that time. Collections made after 1960 were seen from Massachusetts, New Hampshire, Vermont, Wisconsin, and Ontario; label data suggest that most of them represent naturalized populations.

Figure 3 summarizes the distribution of *G. muralis* in Michigan, including both specimens and literature citations unsubstantiated by specimens. Specimens examined from Michigan are listed below. Symbols for herbaria follow Holmgren & Keuken (1974); numbers in square brackets indicate the number of specimens at the cited herbarium.

INGHAM CO.: Agricultural College, *Beal s. n.,* 16 Sept. 1900 (CAN); near (N.W.) Greenhouse, Michigan Agricultural College, *Beal,* 16 Oct. 1900 (MSC). MANISTEE CO.: roadside, Manistee, *Daniels,* June 1900 (UMO). MUSKEGON CO.: sandy streets, Montague,

Fig. 3. Michigan distribution of *Gypsophila muralis* based on herbarium specimens. Stars indicate unconfirmed records.

Hill 183/1899, 14 Aug. 1899 (F[2], ILL[2]; see Hill, 1900); in dry sand, streets of Montague, *Hill,* 14 Aug. 1899 (NY) [probably a duplicate of the other Hill collection].

The E. J. Hill collections at Montague are the first in the Great Lakes area, predating records from Wisconsin by four years (Schlising & Iltis, 1962) and Minnesota by 11 years (*Chandonnet* in 1910, IND, MIN). A portion of a letter from Hill attached to the specimen at NY (see Fig. 1) reads:

> I enclose a little plant which I took from a little used street of Montague, Mich., a village opposite Whitehall. I am not quite sure if it is Gypsophila muralis L. or some other garden form. It was very diffuse or prostrate-spreading, growing in dry sand. In habit it seems something like G. repens as I find described in Nicholson's Dict. of Gard. It was in a quite dense mat.

The next citation of *G. muralis* in Michigan, in Britton (1901), was probably based on this collection. Daniels (1904) considered *G. muralis* to be an escape and listed its occurrence as "Streets, rare." Beal (1905) listed the Manistee collection by Daniels as the only record for the state. No mention was made of his East Lansing collections or Hill's collections. Since the species is not asterisked in his list, I assume that he considered *G. muralis* to be neither indigenous nor naturalized in the Lansing area. Gates (1916) listed the species for North Fishtail Bay (Douglas Lake, Cheboygan Co.), but later listed *G. paniculata* instead (Gates & Ehlers, 1925); the latter agrees with the identity of the specimen (*McFarland* in 1915, UMBS) cited in Gates (1916). Brown (1937) stated that *G. muralis* is "in cultivation at Rock Harbor" (Isle Royale), but his specimen (*Brown 3592* in 1930, MICH) is not *G. muralis.* Two references to *G. muralis* remain unsubstantiated by specimens. Graham (1921) listed the species for Lake Harbor, near Muskegon, and Dodge (1921) stated that it is well established and plentiful in an old field at Misery Bay near Alpena, an area he probably surveyed in 1912 or 1913.

Visits to selected areas cited above in the summer of 1978 proved to be futile: the greenhouse Beal referred to was dismantled before 1915 (Beal, 1915); most of the village of Montague has been extensively disturbed by recent sewer construction; and shoreline development has made access to portions of Misery Bay difficult. A survey of Lake Harbor and portions of Manistee revealed no *G. muralis.* An additional survey of Montague and closer inspection of the numerous populations of *Petrorhagia saxifraga,* the "look-alike," in Manistee during August of 1979 disclosed no evidence of *G. muralis.* Michigan is listed in *The New Britton and Brown Illustrated Flora* (Maguire, 1952) as an area where *G. muralis* is established locally as a weed; this reference I feel is a holdover from Britton (1901). No mention of such an occurrence is found in *Gray's Manual of Botany* (Fernald, 1950). A visit to Portage and Marathon Cos., Wis., in August 1980 revealed *G. muralis* growing in dry sand of park lawns and some roadsides. The sites are very similar to those occupied by *Petrorhagia saxifraga* in Michigan, suggesting that *G. muralis* could be present here, although no naturalized populations are now known in Michigan.

CAN, CM, CU, DAO, DS, F, GH, HAM, ILL, IND, LL, MASS, MIN, MO, NA, NCU, ND, NEBC, NHA, NY, PENN, PH, POM, SMU, TEX, UMBS, UMO, US, VT, and WIS. I appreciate the hospitality of the curators of BLH, EMC, F, HAM, HHH, MICH, MO, NYS and UWSP during visits there.

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VEGETATIONAL STUDIES ON TULIPTREE STANDS IN SOUTHEASTERN MICHIGAN

Paul W. Thompson

Cranbrook Institute of Science
Bloomfield Hills, Mich., 48013

In Michigan, tuliptree reaches its northern limit in the southern part of the state where it normally grows adjacent to and somewhat above areas where the water level is close to the surface. As little quadrat data have been collected on natural stands in which tuliptree is dominant and many such habitats are being destroyed, it is desirable to record data on these stands.

Two types of communities were selected. One, representing a typical tuliptree habitat, is located at the Haven Hill section of the Highland Recreation Area (White Lake Township, Oakland Co., SW¼ of NE¼, sect. 29), where earlier studies were made by the writer (1953). Only a foot or two higher than its surroundings, the stand occupies a small "island" of Houghton muck in the midst of a swamp forest. The second area, unusual in having beech as a major associate, is located in the Belleville area (Wayne Co., between Lenmore and Haggerty Roads, 0.5 km. N of Savage Road). On an old glacial lake plain, this area is essentially flat and drier than the first site. Two sectors (NE ¼ of NE ¼, sect. 26, Van Buren Twp.) were selected in the main portion of the forest: Sector I—near the southeastern corner of the woods; Sector II—near the eastern border, in the middle portion of the stand. The soil consists of Thetford sandy loam. Sector III (NW ¼ of NW ¼, Sect. 25) was chosen for comparison as the composition is different, beech being a major component, tuliptree a minor constituent. The soil at Sector III consists of Gilford sandy loam; the site is slightly higher.

Using methods of earlier studies (Thompson, 1963), seven 10 X 10 m quadrats were set up at Haven Hill in 1975; at Belleville Woods, in 1977, 5 X 5 m quadrats were laid out (36 in Sector I, 30 in Sector II, and 30 in Sector III). The circumference at breast height (CBH) of trees with a diameter exceeding 5 cm (2 in.) was measured with a steel tape. The height of taller trees was measured with an Abney hand level. The basal cross-sectional area for each tree in the canopy layer was calculated from the circumference value. The relative coverage for each species was calculated by dividing the total basal areas of all trees of that species by the grand total basal areas of all trees. The relative coverage is used as a measure of dominance (Tables 1−2).

Trees noted in the various plots are as follows:

ash, black (*Fraxinus nigra*)
ash, white (*F. americana*)
basswood (*Tilia americana*)
beech (*Fagus grandifolia*)
birch, yellow (*Betula lutea*)
blue beech (*Carpinus caroliniana*)
cherry (*Prunus* sp.)
dogwood, flowering (*Cornus florida*)
elm, white (*Ulmus americana*)

gum, black (*Nyssa sylvatica*)
hickory, bitternut (*Carya cordifolia*)
ironwood (*Ostrya virginiana*)
maple, red (*Acer rubrum*)
oak, red (*Quercus borealis*)
oak, white (*Q. alba*)
sassafras (*Sassafras albidum*)
tuliptree (*Liriodendron tulipifera*)

Fig. 1. Beech wood at Belleville.

In the Haven Hill tract, tuliptree provides 50% of the coverage, red maple 25%, and white ash 18%. Minor constituents are beech 4%, black ash 2%, and bitternut hickory 0.5%. The understory consists principally of ironwood and blue beech mixed with transgressives such as basswood, red maple, white elm, and white ash. The shrub layer is composed of gooseberry (*Ribes cynosbati*), mapleleaf viburnum (*Viburnum acerifolium*), alternate leaf dogwood (*Cornus alternifolia*), spice bush (*Lindera benzoin*), common elder (*Sambucus canadensis*), and transgressives of the canopy species. In this habitat, the dominance of tuliptree is clearly illustrated; red maple and white ash are co-dominants.

In Belleville Woods, Sector I consists of red maple 30%, tuliptree 23%, and beech 20% as dominants, with red oak 14% and white oak 12% as minor constituents. In Sector II, the dominants are beech 56%, red maple 23%, and tuliptree 19%, with sassafras 2% as a minor component; in both sectors the dominants are the same. Combining Sectors I and II gives coverage values of

beech 32%, red maple 28%, tuliptree 22%, red oak 9% and white oak 8%. The understory of Sector I is ironwood, blue beech, and transgressives of the canopy layer; that of Sector II is composed of ironwood and transgressives of beech, red maple, sassafras, and elm. The shrub layer of the two sectors consists largely of transgressives of ironwood, beech, and red maple, with some blue beech in Sector I and sassafras in II. The coverage of Sector III is primarily 56% beech with substantial amounts of black gum (19%), red maple (15%), and white ash (10%). The understory is made up of flowering dogwood and transgressives of the canopy species. The shrub layer is composed of transgressives of these same species, beech being particularly plentiful.

The ground cover of Belleville Woods (especially rich in spring species) includes as common plants yellow trout lily (*Erythronium americanum*), Canada mayflower (*Maianthemum canadense*), solomon seal (*Polygonatum pubescens*), jack-in-the-pulpit (*Arisaema triphyllum*), early bedstraw (*Galium aparine*), and Virginia creeper (*Parthenocissus quinquefolia*). Other species include spring beauty (*Claytonia virginica*), wild geranium (*Geranium maculatum*), large white trillium (*Trillium grandiflorum*), may apple (*Podophyllum peltatum*), white baneberry (*Actaea alba*), stemless blue violets (*Viola sororia* and *V. papilionacea*), smooth yellow violet (*Viola eriocarpa*), and nodding bellwort (*Uvularia sessilifolia*). Less frequent species are wild strawberry (*Fragaria virginiana*), Indian cucumber-root (*Medeola virginiana*), carrion flower (*Smilax* sp.), and creeping wahoo (*Euonymus obovatus*).

Sectors I and II have as dominants tuliptree, red maple, and beech. They differ considerably from the stand at Haven Hill in having beech as a co-dominant. Drier, sandy soil at Belleville may be responsible for such a difference

TABLE 1. Composition of tuliptree community at Haven Hill. Seven 10 × 10 m quadrats

Species	Measure										Total	% Coverage
Tuliptree	Ht. (m)	32	33	36	33	31	32	35	33	33		
	CBH (cm)	114	157	157	160	160	163	170	170	178		
	Basal area (m²)	15	28	28	29	29	30	33	33	36	261	50.2
Red Maple	Ht. (m)				27		33	35				
	CBH (cm)	64	79	91	102	158	168	178				
	Basal area (m²)	5	7	10	12	28	32	36			130	25.0
White Ash	Ht. (m)	30	28	35	34							
	CBH (cm)	91	132	162	178							
	Basal area (m²)	10	20	30	36						96	18.5
Beech	Ht. (m)	17	22									
	CBH (cm)	41	125									
	Basal area (m²)	2	18								20	3.8
Black Ash	Ht. (m)	21	22									
	CBH (cm)	66	74									
	Basal area (m²)	5	6								11	2.1
Bitternut Hickory	Ht. (m)	20										
	CBH (cm)	46										
	Basal area (m²)	2									2	0.5
	Total:										520	100

TABLE 2. Composition of hardwood forest at Belleville

Sector I: 36 5 × 5 m quadrats in the southeastern section of woods

																Total	% Coverage
Red Maple	Ht. (m)	13	15				17	19	22	24		27		25	32		
	CBH (cm)	38	38	48	48	53	61	66	69	79	79	97	107	185	263		
	Basal area (m²)	2	2	3	3	3	4	5	5	7	7	11	13	39	64	168	29.7
Tuliptree	Ht. (m)		22	34	32	34											
	CBH (cm)	51	76	165	183	203											
	Basal area (m²)	3	7	31	38	52										131	23.1
Beech	Ht. (m)		29	34													
	CBH (cm)	84	173	251													
	Basal area (m²)	9	34	72												115	20.3
Red Oak	Ht. (m)	34															
	CBH (cm)	259															
	Basal area (m²)	77														77	13.6
White Oak	Ht. (m)	36															
	CBH (cm)	239															
	Basal area (m²)	94														65	11.5
White Ash	Ht. (m)	28															
	CBH (cm)	91															
	Basal area (m²)	10														10	1.8
															Total:	566	100

Sector II: 30 5 × 5 m quadrats in the east-central section of woods

									Total	% Coverage
Red Maple	Ht. (m)			22	23	23	26	28		
	CBH (cm)	48	51	69	69	71	112	165		
	Basal area (m²)	3	3	5	5	6	14	31	68	23.3
Tuliptree	Ht. (m)	25	30	28						
	CBH (cm)	91	135	147						
	Basal area (m²)	10	21	25					55	18.8
Beech	Ht. (m)	15	24	31	35					
	CBH (cm)	48	183	211	252					
	Basal area (m²)	3	38	51	73				164	56.2
Sassafras	Ht. (m)	19								
	CBH (cm)	64								
	Basal area (m²)	5							5	1.7
								Total:	292	100

Sector III: 30 5 × 5 m quadrats in the eastern part of the woods

													Total	% Coverage
Beech	Ht. (m)	23	28	29	19	29	32	33	36	24	34	35		
	CBH (cm)	127	142	155	160	165	178	180	188	193	206	221		
	Basal area (m²)	19	23	28	29	31	36	37	40	43	49	56	391	56.2
Black Gum	Ht. (m)			14	26	30	27							
	CBH (cm)			48	142	183	244							
	Basal area (m²)			3	23	38	68						132	19.0
Red Maple	Ht. (m)			22	30	35								
	CBH (cm)			81	140	257								
	Basal area (m²)			8	22	76							106	15.2
White Ash	Ht. (m)			23	35									
	CBH (cm)			109	216									
	Basal area (m²)			14	53								67	9.6
												Total:	696	100

in composition. It is of interest that sugar maple, often associated with beech in southern Michigan, was not found at the Belleville site. Sector III has beech co-dominant with red maple, but tuliptree is replaced by black gum and white ash. A slightly higher elevation and a slight difference in the soil may account for the different composition, although both black gum and white ash grow well in moister situations.

The Haven Hill tract is preserved as a Nature Study Area. It would be desirable to preserve Belleville Woods so that long-range studies could follow changes occurring there.

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The October issue (Vol. 19, no. 4) was mailed January 16, 1981.

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On the cover: *Hoarfrost*
on sugar maple, Chippewa Nature Center,
Midland, January 1980; photo by Doug Moore

COR/STA

THE

MICHIGAN BOTANIST

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Membership in the Michigan Botanical Club is open to anyone interested in its aims; conservation of all native plants; education of the public to appreciate and preserve plant life; sponsorship of research and publication on the plant life of the State; sponsorship of legislation to promote the preservation of Michigan native flora and to establish suitable sanctuaries and natural areas; and cooperation in programs concerned with the wise use and conservation of all natural resources and scenic features.

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A NATURE TRAIL FOR THE BLIND

Susan Buyze

1572 Pearl St.
Benton Harbor, MI 49022

The development of a nature trail for the blind was a recent undertaking of the Western Michigan University chapter of Beta Beta Beta, a national biological society. Because of the uniqueness of the project and enthusiastic response to it, we would like to share our experience in producing it.

It was first necessary to choose a location for the trail with regard to the availability of features of interest and the relative ease with which a blind person could locate the trees. Our trail was developed on the grounds of the Kalamazoo Regional Psychiatric Hospital, directly across the street from the Michigan Rehabilitation Center for the Blind. The hospital grounds were designed many years ago with use as an arboretum in mind. They are flat, with no brush or fences between the trees, and sidewalks allow ease of movement.

Trees were chosen on the basis of proximity, uniqueness, ease with which they could be distinguished by touch, and variety of types available. We chose 26 trees and plotted their exact locations on a map so that we could relocate them after identification plaques had been made. (The Hospital had maps of the grounds which could be used.)

Descriptions were written with emphasis on traits that could be used to identify the trees by touch. We also detailed the potential uses of each tree. We then designed plaques consisting of a 12 × 12 inch plywood backing coated with urethane and a clear sheet of plexiglass on which a braille message was inscribed (by the Michigan Braille Transcribing Service, 4000 Cooper St., Jackson,

MI 49201). Sandwiched between the plexiglass and the plywood was a laminated sheet of paper with a typewritten message for a sighted person to read. The plexiglass was screwed to the plywood and sealed with clear silicone caulk. The plaques were attached to the trees with 2½ in. lag bolts.

Altogether the project cost $165 (1979 prices). Most of the money was used for construction of the plexiglass plaques. A small amount was used for the plywood backing and supplies used in attaching the plaques to the trees.

In order to introduce our trail to the community, we held a public dedication which received considerable attention from local radio, television, and newspapers.

The accompanying photographs, taken by Clayton Alway, show the identification of an Ohio Buckeye and an Austrian Pine. Mr. Alway wrote, in a letter accompanying the photographs: "The girl is Udell Useen, a student from Ann Arbor. The man is John Boes, an instructor from Kalamazoo. Both are blind. She had no trouble reading the plaques and seemed to enjoy doing so. John Boes commented that it was a very nice place and that he could hear and locate the trees as he approached them. Unfortunately neither of the people could have found the marked trees without help, although John quickly located the plaques and asked if I could read them too and was pleased that I could. I think it would be a valuable experience all around if students from Western would volunteer to act as guides for groups of people from the blind school."

REVIEW

USE OF PLANTS FOR THE PAST 500 YEARS. By Charlotte Ericksen-Brown. 1979. [xxiv] + 510 pp. $14.95 Can. funds. Breezy Creeks Press; Box 104, Aurora, Ontario, Canada L4G 3H1.

This book is basically an extensive compilation of citations, quoted in their original form, about the uses of plants for the past half-millenium. For each of hundreds of species, numerous citations are listed in chronological order describing past use of the plants for food, fuel, fiber, shelter, utensils, medicine, and clothing. The area covered is northeastern North America, from Missouri eastward to the Atlantic and north to the arctic. Each plant is briefly described to help with field identification, and line drawings are included. Species are grouped into four basic categories, evergreen trees, deciduous trees, shrubs and vines, and herbs, with exceptions as noted in the table of contents. The herbs are subdivided according to habitats. A brief glossary is included, as well as an impressive bibliography of about 444 titles.

The book is a gold mine of information. Widely scattered snippets of information in original sources and often difficult-to-obtain literature have been brought together in a compact volume. No doubt there have been omissions, but still the book is well worth the money for people with an interest in uses of wild plants. The citations for each species run from early uses by native peoples all the way to recent medical research. In interpreting the older uses, the author must have faced great problems in discerning what plants were intended. There will undoubtedly be room for differences of opinion here, but it appears that the basic research has been well done.

The type face of the book is comfortably readable. The book is sturdily bound in a water resistant paper cover and looks like it would wear well. The illustrations are fairly well reproduced, and typographical errors are relatively few. One potential problem is that the margins of the book are so narrow that if it became necessary to re-bind the volume, there would be precious little to spare for re-trimming. Also, marginal notes are impossible.

While perhaps not fully realizing the author's aim that this be basically a field guide, and probably too costly and heavy to take backpacking, this book nevertheless will be a valuable and interesting addition to the naturalist's reference library.

Susan A. Reznicek

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BOTANISTS AND NATURALISTS AT WISCONSIN DELLS
IN THE 19TH CENTURY

Kenneth I. Lange

Dept. of Natural Resources,
Devil's Lake State Park, Baraboo, Wis., 53913

In south-central Wisconsin the Wisconsin River flows through an area of sandstone outcrops, with a series of narrow, east-west trending ravines or gorges leading into the main channel, especially in the upper reaches. This is the famous Wisconsin Dells or Wisconsin Dalles region (not to be confused with the Dalles of the St. Croix River along the Wisconsin-Minnesota border). The gorges, with their drainage of cold air, and certain other exposures harbor a number of boreal plants, for example, sword moss (*Bryoxiphium norvegicum*), fragrant fern (*Dryopteris fragrans*), and Lapland rosebay (*Rhododendron lapponicum*). This region became known to the botanist and naturalist, as well as the tourist, at an early date. This review traces some of the initial botanical exploration.

More than a century ago, in 1868, a pioneer photographer, H. H. Bennett, began taking landscape pictures of the Dells (Rath, 1979, pp. 28–30), and it was largely through his efforts that the region became well known. Five years later the Dells had its first regular steamboat service (Bennett, 1969), and in the following year, 1874, Bennett sold more than 20,000 copies of stereos and was issuing 40 new views (Rath, 1979, pp. 34–35). By 1888, in an outdoor recreation magazine, the Dells was being referred to as the "wonderland of Wisconsin and the north," a "Mecca" for the tourist, sportsman, painter, poet, reporter, geologist "with bag and hammer," and "equally enthusiastic botanist, who here finds a vast natural fernery where a great variety of the rare green beauties may be obtained for the plucking" (Lear, 1888, p. 159). At least one of these "rare green beauties," fragrant fern, is now unequivocally rare in the Dells, largely because of indiscriminate "plucking" (Lange, 1979).

The first botanist to visit Wisconsin must have been Thomas Nuttall (Lapham, 1853, p. 375), but he did not tour the Dells. Nuttall's route in Wisconsin was the Fox-Wisconsin waterway (Graustein, 1951, pp. 68–70; 1967, pp. 52–54).

Increase Allen Lapham (1811–75) apparently was the first botanist to visit the Dells. Lapham was one of Wisconsin's most remarkable citizens; his range and depth of interests remind one of Thomas Jefferson. Lapham was Wisconsin's first resident botanist, indeed, first scholar in a number of fields. Here was a man who compiled a flora of Wisconsin, studied fossil animals, made geological reconnaissances, published maps of Wisconsin, pioneered in the surveying of Indian mounds, devised a weather warning system, and argued for wise use of natural resources (Clark, 1957; Scott, 1975; Voss, 1978, pp. 29–33). In researching Lapham material, one becomes increasingly aware of the universal respect accorded him by his peers. To Asa Gray of Harvard, for example, Lapham was "thoroughly to be respected, and implicitly to be relied upon:—a modest, retiring, industrious, excellent man" (cited by Clark, 1957, p. 20).

In his Plants of Wisconsin, Lapham listed 949 species (933 vascular and 16 non-vascular), "all found within thirty miles of the city of Milwaukee, unless other localities are mentioned" (1853, p. 376). One of these "other localities" was the Dells of the Wisconsin River, which Lapham first visited in 1849 (Lapham, 1849). He defined the Dells as the region "from near the mouth of the Lemonweir, ten miles above the Dell house [a hotel formerly located on an island upriver from the city of Wisconsin Dells] to the mouth of Dell creek four miles below, having, therefore, a length of about 14 miles." On the vegetation of the Dells he commented: "We find here the white, [red and jack pine], the hemlock & cedar &c. Among the shrubs we notice [sweet fern, *Comptonia peregrina*], not before credited to Wisconsin." Listed in his 1853 state flora as occurring at the Dells are three ferns, Labrador tea (*Ledum*), and arctic primrose (*Primula mistassinica;* credited to Mr. B. F. Mills).

Hale & Lapham (1858) cited eight additional species of vascular plants from the Dells, all collected by Lapham: two ferns, a grass and two sedges, an evening-primrose, a St. John's-wort, and *Sullivantia.* Asa Gray was excited

Taylor's Glen.   Kilb'n City.   No. 6.

Fig. 1. Increase Lapham at Wisconsin Dells in 1869 (standing). The man sitting is Alanson Holly, editor of the Wisconsin Mirror, a Dells newspaper of those years. A stereo view by H. H. Bennett. From the collections of the State Historical Society of Wisconsin.

Fig. 2. A field collector's equipment of a century ago: Lapham's vasculum, rule, and plant press. From the collections of the State Historical Society of Wisconsin.

about this record of *Sullivantia*. "A great find it is," he wrote Lapham, "that of *Sullivantia* in Wisconsin" (Gray, 1858).

The University of Wisconsin Herbarium has Lapham specimens from the Dells which were collected in 1861 (e.g., the grass, *Calamagrostis inexpansa*), 1869 (e.g., painted-cup, *Castilleja sessiliflora*), and 1872 (e.g., fragrant fern).

Lapham apparently was the first to report fragrant fern for Wisconsin Dells, and also for the Penokee Range in northern Wisconsin. Several noteworthy people were involved with Lapham because of this fern. Sir William Hooker of the Royal Botanic Garden at Kew wrote Lapham about fragrant fern (Hooker, 1859), and John Muir, "John of the Mountains" (1838–1914), visited the Dells in 1867 because of information from Lapham (through an intermediary) that fragrant fern grew there in the ravines. Muir and his companion found it in at least one gorge and "pronounced its odor most entrancing" (Wolfe, 1978, pp. 107–108).

Of the ravines, Muir wrote: "No human language will ever describe them." But he tried: [These] "are the most perfect, the most heavenly plant conservatories I ever saw. Thousands of happy flowers are there, but ferns and mosses are the favored ones." He concluded his letter with this comment: "We

cannot remove such places to our homes, but they cut themselves into our memories and remain pictured in us forever" (Muir, 1867; see Wolfe, 1978).

Muir and his companion stayed overnight in the Dells, then, in characteristic Muir fashion, built a raft and floated the Wisconsin River to Portage, some 20 miles away. The young Muir lost his shoes enroute and arrived in Portage barefooted and wild-looking. This inventor and university student would soon leave the midwest for California, to become eventually the "grandest character in national park history" and one of America's outstanding naturalists (Wolfe, 1978, 1979).

Hale (1860) listed three vascular plants from "Kilbourn City" (= Wisconsin Dells), presumably collected by the author: club-spur orchid, *Habenaria clavellata* (cited as *Gymnadenia tridentata*), and two blueberries, including the northern *Vaccinium cespitosum*. The only Hale specimens from the Dells that I have found at the University of Wisconsin Herbarium were collected in 1861. They include a sedge (*Carex oligosperma*), colic-root (*Aletris*), two orchids (*Malaxis unifolia* and *Pogonia*), a sundew (*Drosera rotundifolia*), yellow birch (*Betula lutea*), and dwarf bilberry (*Vaccinium cespitosum*). Some of them, notably the *Vaccinium,* have not been relocated, but it should be kept in mind that labelling in those years was imprecise: "Kilbourn" or "Kilbourn City" might have encompassed a huge area.
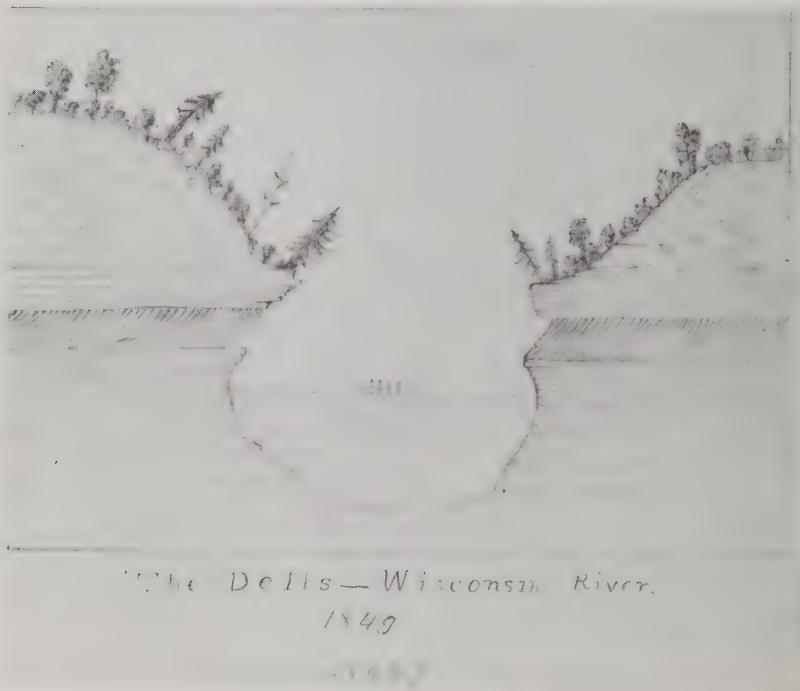

Fig. 3. Wisconsin Dells as depicted by Lapham in 1849. From the collections of the State Historical Society of Wisconsin.

Fig. 4. Here in the Narrows the Wisconsin River turns sharply and is constricted to a width of some 50 feet. In the lumber rafting days, this was the "Raftsmans' Terror." Looking upriver, October 1974. For other views of this spot, see Rath, 1979, pp. 10, 168, 174, 185.

An aura of mystery surrounds Thomas J. Hale, collector of plants and fossils in the upper midwest, mainly Wisconsin, from approximately 1860 to 1862. This young man found himself out of a job when the legislature abolished the state geological and agricultural survey in 1862, and also he had disagreements with James Hall, the survey chief. Apparently the last anyone ever heard of him was an 1862 letter to Lapham, postmarked New York (Hale, 1862). Perhaps he served and died in the Civil War. In 1876 he was referred to as the lamented T. J. Hale (Copeland, 1876). For more information on Hale, see Musselman (1969).

Herbert E. Copeland (1849–76), an instructor at schools in Wisconsin, Illinois, and Indiana, visited the Dells more than a century ago; like Hale, he died young. His 1876 paper was published shortly before his death. At the Dells he found several interesting vascular plants not heretofore reported: Hooker's orchid (*Habenaria hookeri*) and twin-flower (*Linnaea*).

One of the most exciting botanical discoveries at the Dells occurred in 1883, when Elizabeth G. Britton (1858–1934) found the sword moss in fruit. This was the first time that capsules of this rare species had been reported. Fruiting specimens were again found at the Dells by L. S. Cheney in 1894. Apparently these remain the only instances where this moss has been found in fruit (Knight, 1883; Britton, 1897; John W. Thomson, Jr., pers. comm.). This discovery started Mrs. Britton, then Miss Knight, on her career as a professional

bryologist. She eventually became curator of the moss collections at the New York Botanical Garden. (Her husband was Nathaniel Lord Britton of the Britton & Brown Illustrated Flora.)

Lellen Sterling Cheney (1858–1938) was in charge of the University of Wisconsin Herbarium from 1891 to 1903. His special interest was the Wisconsin River Valley, where at "Delton, Wis." (the Lower Dells) in 1899 he collected the lance-leaved violet (*Viola lanceolata*). A contemporary, Rodney H. True (1866–1940), was a plant physiologist who in the 1880's and 1890's collected in the Dells and also in the Baraboo Hills south of the Dells, including the Devil's Lake area. He found Selkirk's violet (*Viola selkirkii*), a boreal species, at the Dells, and it was Cheney and True, in 1897, who discovered Lapland rose-bay at the Dells (True, 1898). This arctic-alpine rhododendron had not previously been found in the United States west of the Adirondack Mountains. It is now known from one other site in Wisconsin. This is an especially dramatic example of disjunct distribution, as these localities are separated from the eastern mountain stations and the most southerly arctic stations by approximately 800 miles in both cases (Read & Wrzesinski, 1878).

For further information on pre-1900 work on the Wisconsin flora, see the review by Cheney (1900–01).

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SEED DISPERSAL BY FALLING WATER DROPS

D. B. O. Savile

Biosystematics Research Institute
Agriculture Canada
Ottawa, K1A 0C6, Canada

The note by Gladstone (1980) on seed dispersal in *Mitella nuda* unfortunately does not distinguish between active dispersal and passive release. The function of short-range dispersal is to take the disseminule away from the base of the parent plant. Splash dispersal does function well in *Mitella nuda,* as in other species of the genus, and in other plants with the typical flared cup (examples given in Brodie, 1975). However, it is possible for lack of appropriate drops to delay discharge; and the capsule may then evert and the seeds fall passively, with some chance of establishing seedlings. The lowest capsule in Gladstone's figures is certainly in this condition.

A partly quantitative discussion of dispersal by splash-cup and springboard is given by Savile & Hayhoe (1978) and Savile (1979).

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REVIEW

TREES AND SHRUBS FOR NORTHERN GARDENS, by Leon C. Snyder. 411 pp. + 96 pl.
    University of Minnesota Press, Minneapolis, 55414. 1980. $17.95.

Here is a book for all gardeners and landscapers in the northernmost parts of the
United States and adjacent Canada. The aim of the book is to provide accurate information
on plants that can be grown in northern gardens and their relative hardiness and cultural
requirements. Use of this book should prevent the all too common sights of Forsythias that
do not bloom above the snowline, ugly, winterburned evergreens, and brushy, half-dead,
winterkilled trees and shrubs.

Introductory material deals with morphology, nomenclature, culture, and hardiness,
as well as selection of plants for particular landscape purposes. At the end of the book is a
glossary and selected bibliography. The main body of the text is a treatment of about 400
species of woody plants that are useful for northern gardens. There are keys to genera and
species, and the plants are arranged alphabetically by Latin name. Common names are
cross-referenced for easy use. For each species, there is a short description and a paragraph
detailing cultural requirements, propagation, and use of the plant, followed by a list of
cultivars or varieties, if any. (Cultivars not assignable to a species are placed at the end of
the genus.) A major portion of this section of the book is occupied by 96 pages of color
photographs.

A great value of this book is that the species selection and cultural suggestions are
directed towards gardeners in zones 2, 3, and 4 (USDA map). Also, much of the information
is apparently original and based on the performance of the plants at the University of
Minnesota Landscape Arboretum. Although the book deals extensively with such main-
stays of northern gardens as Crabapples, Lilacs, and Honeysuckles, gardeners in the north
will be surprised at the number of seemingly exotic species that they can grow, including
(for zone 4) six species of *Aesculus,* seven of *Magnolia,* and such interesting trees and
shrubs as *Maackia amurensis, Taxodium distichum,* and *Abeliophyllum distichum.* The se-
lection of species treated seems quite reasonable. Of course, there exist hundreds of other
woody plants that would be hardy, but these are often of little horticultural interest or, in
some instances, essentially unavailable. Quite gratifying is the number of native species in-
cluded. The color photographs, 384 in all, are generally good and will be helpful in selecting
and identifying plants. The cultural hints provided at the front will also be helpful. Sugges-
tions on mulching, providing winter shade to broad-leaved evergreens (and some conifers),
and wrapping tree trunks will prevent much winter damage to plants in northern gardens.

Perhaps the most serious omission is the lack of mention of the substantial amount
of documentation of hardiness and listing of hardy species done by Canadian workers.
References such as *Ornamental Shrubs for Canada* (Lawrence C. Sherk & Arthur R.
Buckley, Can. Dept. Agr. Publ. 1286, 1968) and *A Checklist of Ornamental Trees for
Canada* (Lawrence C. Sherk, Can. Dept. Agr. Publ. 1343, 1971) are not in the bibliography.
Some trees and shrubs reported in these references that would appear to be hardy enough
to be included in this book are not listed. Examples of fine ornamentals in this category
include, among others, *Catalpa ovata, Juglans ailanthifolia, Kalopanax pictus, Quercus
imbricaria, Cotoneaster dielsiana, Cytisus nigricans, Genista sagittalis,* and *Viburnum
sieboldii.*

Overall, the book is organized for easy reference, appears well bound, and has
relatively few typographic errors.   —A. A. Reznicek

SOME SPECIES OF LEUCOCOPRINUS WHICH GROW IN GREENHOUSES

Helen V. Smith

Matthaei Botanical Gardens and University Herbarium
University of Michigan, Ann Arbor, 48109

The mushrooms comprising Stirps Cepastipes grow primarily in tropical or warm regions and in greenhouses in more northern areas. Over a period of years four species of *Leucocoprinus* have been found to fruit in greenhouses at the University of Michigan's Matthaei Botanical Gardens. These (one of which is described as new) and two species found in greenhouses on the west coast and elsewhere are described here. Of the included species one grows outdoors in southern Michigan, and it and others grow outside in warmer parts of the country.

The genus has not been treated monographically but some authorities recognize two or more divisions. The species included here belong to a single stirps (Cepastipes) centered around *Lepiota cepastipes,* the type species of the genus. They resemble the thinner *Coprini* in having very thin flesh and a plicate-striate to sulcate pileus margin. The lamellae are usually remote from the stipe by a broad smooth band. The spore print is white to yellowish-white, and the spores have a distinct to indistinct germ pore, or none; spore size may be quite variable. In some species the hymenium is quite similar to that in *Coprinus* and *Psathyrella.* Basidia and brachybasidioles are similar and narrowly clavate at first. The brachybasidioles become swollen and broadly oval or saccate but do not increase in length. The basidia may elongate and at maturity protrude from the hymenium for half their length; they become cylindric or somewhat ventricose near the middle, and in some species the basal portion becomes so compressed as to appear stalklike. Cheilocystidia are abundant, mostly clavate to fusoid-ventricose, with or without an apical protuberance. Pleurocystidia are absent to very rare and like the cheilocystidia. Clamp connections are absent or very rare. (A diagram illustrating hymenial elements is given in fig. 1.)

Color names in quotation marks are from Ridgeway.

|		
1	Fruiting body predominantly yellow	2
1	Fruiting body not yellow	5
	2 Spores mostly 8−11 µm long	3
	2 Spores mostly 3.6−6.6 µm long	4
3	Pileus with gray-brown disc and scales; base of stipe bright cadmium-yellow, sometimes also with gray-brown scales	*L. tricolor*
3	Fruiting body evenly yellow over all, or if some brown present then a reddish- or yellowish-brown	*L. birnbaumii*
	4 Pileus surface yellow over all (disc may be more deeply colored): spores mostly 3.6−4.5 µm long	*L. denudatus*
	4 Pileus surface greenish-yellow, the disc brown and glabrous (contrasting strongly with the rest of the surface); spores mostly 4.8−6.8 µm long	*L. flavescens*
5	Pileus with brown ("bister") disc, the scales brownish and quite distinct; spores mostly 9−12 × 7−9 µm	*L. brebissonii*
5	Pileus white to dingy-white, disc usually only slightly darker (rarely brownish), the scales not distinctly colored; spores mostly 7−9 × 6−7.5 µm	*L. cepastipes*
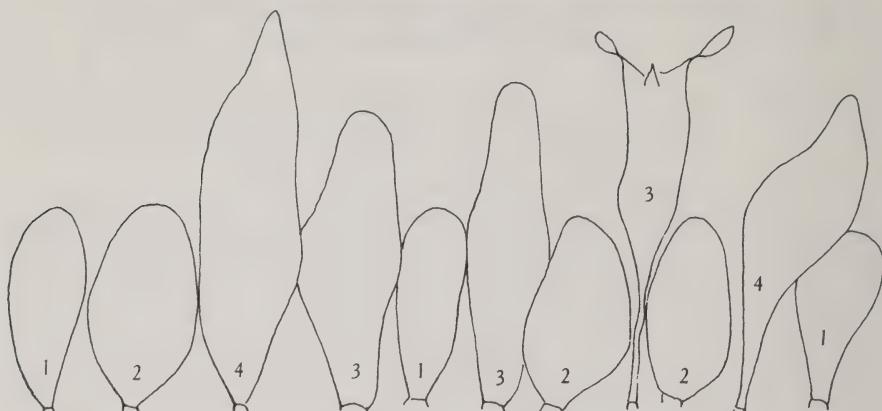
Fig. 1. Elements of the hymenium: 1, young basidia; 2, brachybasidioles; 3, basidia; 4, cystidia.

Leucocoprinus tricolor sp. nov.   Fig. 2

Pileus 1.6–6 cm latus, ovatus demum campanulatus vel late expansus, flocculoso-squamulosus, ad centrum griseo-brunneus, ad marginem luteus, demum sulcato-striatus; odor pungens; gustus mitis. Lamellae confertae demum subdistantes, latae, pallide citrinae. Stipes 1.5–6 cm longus, 2–6 mm crassus, ad basin 6–11 mm crassus, sursum citrinus, deorsum aurantiacus annulatus. Sporae 8–11 $\times$ (6)7.2–9 μm, ellipsoideae vel subglobosae, dextrinoideae. Cheilocystidia clavata, sphaeropedicellata vel vesiculosa; cuticula pilei granulosa. Specimen typicum in Herb. Univ. Mich. conservatum est; legit H. V. Smith no. 507a.

Pileus 1.6–6 cm broad, ovate to campanulate or obliquely conic, nearly plane at maturity with or without a distinct umbo; surface at first finely floccose-squamulose, the squamules over the umbo and those near it grayish-brown, remainder of surface and most of the squamules pale-yellow, umbo sometimes becoming ±glabrous in age and in some young buttons orange-yellow before becoming brownish; distinctly striate to plicate or sulcate toward the margin. Flesh very thin, pliant, dry in texture, pale-yellow with no color change on injury; taste not distinctive, texture when tasted dry and cottony; odor pungent (like that of *Lepiota cristata*), best noticed when a package of fresh specimens is unwrapped.

Lamellae remote from the stipe, close becoming subdistant, broad, very thin, pale lemon-yellow, not spotting, edge even.

Stipe 1.5–8 cm long, 2–6 mm at apex, 6–11 mm thick at base, glabrous or with a few fine scales above and some small floccose scales below, lemon-yellow above, golden-yellow (pale cadmium) near the base, the scales at the base tinged orange or grayish-brown; sometimes turning grayish-brown slowly after handling. Context pale yellow. Annulus small, thin, membranous, yellow, soon evanescent.

Spores 8–11 × (6)7.2–9 μm broadly ellipsoid to subglobose, (rarely some globose or nearly so and 7.2–75 μm in diam.), wall thickened, germ pore small, seen as a small pale spot in Melzer's sol., no lens cap present, wall yellow-brown to dark rusty-brown in Melzer's sol. Basidia mostly 25–29 × 8–10 μm, clavate to fusoid-ventricose, becoming longer and subcylindric and about 45–50 × 7–10 μm, projecting beyond the hymenium for about half their length when mature, sometimes appearing pedicellate as a result of compression of the basal portion in the hymenium; content granular; usually 4-spored but sometimes 2- or 3-spored. Brachybasidioles 12.6–27 × 9–21 μm, narrowly ellipsoid to clavate when young, becoming very broadly clavate to vesiculose when mature, sometimes with a small projection at the apex. Pleurocystidia sporadic to abundant or rare, similar to the cheilocystidia. Cheilocystidia (40)60–74 × 17–30 μm, clavate, sphero-pedicellate, or fusoid-ventricose with or without a small head or 1–3 finger-like projections, filled with a pale yellowish-brown granular content showing Brownian movement, the cheilo-cystidia abundant, often clustered. Lamellar trama very loosely interwoven. Cuticle of the pileus of readily disarticulating cells of various shapes, globose, broadly elliptic, cylindric, oblong-inflated, and various other shapes, some with a gray-brown to yellow-brown content, some with large numbers of small

Fig. 2. *Leucocoprinus tricolor*, H. V. Smith 507a, type (×1), photographed by A. H. Smith.

granules or globules; masses of dark-colored amorphous material sometimes present in the mount (crushed cells?). Hyphae from the base of the stipe containing a bright orange pigment. Clamp connections present on some very narrow (3–4 μm) hyphae but extremely rare.

In clusters or solitary, in a so-called "sterile soil" bin in the greenhouse (at the University of Michigan Botanical Garden) in 1975 and in a few pots of *Hibiscus* for 2–3 years thereafter until the plants were repotted, and in 1980 singly in succession in several pots filled with a bark-based growing mix, also in two pots with regular soil mix. Fruiting January into July.—Material studied: HVS 371, 507, 507a-type, 507b, 509, 510.

As the specimens are drying the 3-color effect often becomes very noticeable (grayish-brown disc or umbo, pale-lemon pileus elsewhere, and orange-cadmium stipe base). A few specimens have been found in which the color is nearly uniform overall, but in these a grayish-tan overlay developed soon after picking. Rarely specimens may become slightly tinged with grayish where bruised or on drying. When specimens are sectioned and mounted in KOH, a yellow pigment diffuses into the medium.

Leucocoprinus birnbaumii (Corda) Sing.
Pileus 3–7 cm broad, ovoid, becoming campanulate to broadly conic to expanded and nearly plane with a prominent umbo, at least the outer third of the pileus distinctly striate, sometimes sulcate in age, surface covered by fine fibrillose to powdery scales overall, the scales easily removed, the umbo densely scaly or infrequently nearly glabrous, color pale lemon-yellow, the umbo tinged with pale yellowish-orange or light-ochraceous ("lemon chrome" to "picric yellow," scales of the disc "yellow ochre"). Flesh very thin and fragile; odor and taste not distinctive or odor slightly pungent.
Lamellae separated from the stipe by a broad, smooth band, crowded, thin, pale-yellow, edge finely fimbriate, concolorous.
Stipe 4–12 cm long, 1–5 mm thick at apex, sometimes slightly enlarged below and then up to 6–8(–14) mm thick, silky to glabrous above the annulus, finely floccose-fibrillose to scaly below, concolorous with pileus above and deeper-colored below, occasionally with some brownish fibrils or scales below. Annulus well formed, membranous to cottony-fibrillose, bright lemon-yellow, flaring upward, movable at least when mature specimens are dried.
Spores 8.4–10.8 × 5–7.8 μm, broadly elliptic in face view, inequilateral in profile, rusty-brown in Melzer's sol., apiculus small, germ pore present. Basidia 4-spored, protruding well out from the hymenium at the time of sporulation. Lamellar trama of somewhat inflated, interwoven hyphae. Pleurocystidia lacking. Cheilocystidia 36–50 × 8–16 μm, clavate to fusoid-ventricose or with an apical projection of some sort, rarely branched at the apex. Pileus trama loosely floccose. Cuticle of the pileus of inflated cells, globose to subglobose to pyriform, 20–30 μm in diam., or irregular in shape, sometimes in chains which separate readily. Clamp connections lacking.

In pots and soil bins, fruiting sporadically in winter and spring. This species has long been present in the University of Michigan greenhouses but has not been observed every

year. According to the former greenhouse superintendent, Walter Kleinschmidt, in some years the mycelium has been so abundant that it bound the soil so much that it had to be stirred with a pitchfork. I have grown perfect specimens by putting some soil with well-dispersed mycelium in a terrarium. When there was sufficient mycelial growth, knots of fluffy, yellow mycelium formed in 2−3 days and fruiting bodies were produced in 10 days to 2 weeks. When some of the yellow to yellow-orange fruiting bodies were dried in silica gel, the scales on the umbo dried a light-brown color.

This species is reportedly poisonous, and so it should not be allowed to fruit in public greenhouses where children might pick and eat the mushrooms. This widely distributed species occurs in the warmer parts of North America and elsewhere.

Leucocoprinus denudatus (Rabh.) Sing.
   Pileus 1.6−2.4 cm broad, ovoid to campanulate or hemispheric, becoming convex-expanded to nearly plane with a decurved margin, the margin striate; disc velvety, remainder of surface slightly pruinose under a lens, pale greenish-yellow ("naphthalene yellow"), the disc a deeper color, the margin paler.
   Lamellae remote from the stipe by a broad smooth band, very crowded, narrow, tinged pale-yellow, edge even, concolorous.
   Stipe 1.5−4.5 cm long, 2−3 mm thick at apex and up to 4−6 mm thick at the base, glabrous to minutely pruinose under a lens, yellow but paler than the pileus, the base often with attached soil. Annulus superior, small, membranous.
   Spores 3.6−4.5 × (3.6)4−4.8 μm (rarely up to 6−8 × 5.2 μm), globose or subglobose to broadly ovoid, very pale-yellow to pale rusty-yellow in Melzer's sol., apiculus minute, germ pore lacking. Basidia 24−36 × 5−8 μm, narrowly clavate, becoming nearly cylindric when sporulating at which time they project from the hymenium for about half their length, many with a granular content. Brachybasidioles present but hard to see. Pleurocystidia lacking. Cheilocystidia 20−34 × 7−10(−14) μm, abundant, fusoid-ventricose with a short to long neck, those with a long neck may have the neck with 1−2 constrictions. Oleiferous hyphae present in the trama. Cuticle of diverse elements; pileocystidia 75−255 × 7−10 μm and tapering to a point occur in clusters; somewhat appressed hyphae with contorted and branched end cells may be filled with numerous fine globules; globose to pyriform cells up to 32 μm in diam. are present in young pilei and on the disc of older ones; the globose cells arise from narrow hyphae about 5 μm in diam. Clamp connections lacking.

   Found only one year, in June, at the University of Michigan Botanical Garden, in dense clusters in "sterile leafmold" and in some flats. This well-known European species has apparently not been previously reported from North America.

When dried one collection had the umbo brown and the rest of the pileus yellow; also some unexpanded pilei dried brownish. The poorly known *Lepiota spectabilis* Clements from a greenhouse in Nebraska may belong here. *L. denudatus* is quite similar to *L. flavescens* except that the disc in the latter is brown and glabrous and contrasts strongly with the rest of the surface, and the spores are usually a little longer.

Leucocoprinus flavescens (Morg.) comb. nov.

> *Lepiota flavescens* Morg., Jour. Myc. 13: 5. 1907.
> *Lepiota allenae* Peck, N.Y. State Mus. Bull. 150: 56. 1911.

Pileus (1.7)2.5—4 cm broad, cylindric-ovate becoming expanded to plane with an obtuse or flattened umbo, plicate-striate almost to the disc, pale greenish-yellow (near "napthalene yellow"), the disc brown and glabrous and contrasting strongly with the rest of the surface, ridges floccose to powdery, the grooves glabrous and white. Flesh thin, white.

Lamellae yellowish, remote from the stipe, close to subdistant, narrow, subventricose.

Stipe 3—6.5(—8) cm long, 2 mm thick at apex, enlarging to 3—5 mm thick at the base, pale sulphur-yellow and covered with fine floccules like the pileus. Annulus superior, pale yellow, delicate and often evanescent.

Spores 4.8—6.6(—7.2) $\times$ (3.5)4.9—5.5 μm, broadly ellipsoid, subglobose or globose, pale yellowish-brown to rusty-brown in Melzer's sol., germ pore lacking. Basidia 15—18 $\times$ 7—8 μm, clavate. Brachybasidioles 14—18 $\times$ 10—15 μm, saccate and thin-walled. Cheilocystidia 17—43 $\times$ 8—15 μm, abundant, clavate, subcylindric, fusoid-ventricose with an obtuse apex, or cylindric with a short neck and a head. Lamellar trama loosely interwoven, oleiferous hyphae present. Pileal trama loosely interwoven, oleiferous hyphae present. Cuticle of pileus a compact layer of enlarged, clavate to pyriform, vesiculose, broadly fusoid-ventricose, or globose, thin-walled cells 10—50 μm broad which may also be found in clusters along the ridges of the striae, but generally not free-floating in the mount. Clamp connections not found.

> Known from a greenhouse in southern California and from one in Massachusetts. This species was described from under trees in southern Ohio but has so far not been found either in the greenhouse or outside in Michigan. Fruiting in July and August.

The description of macroscopic characters is taken from Smith & Rea (1944). Anatomical data are from Rea's collections numbered 1115 and 1116 in the University of Michigan Herbarium. Smith & Rea did not note the reddening of the stipe beneath the cuticle mentioned by Morgan (1907). As suggested by Smith & Rea *Lepiota allenae* Peck, which was found in a greenhouse in Massachusetts, should be regarded as conspecific with *Leucocoprinus flavescens*. A study of the type of *L. allenae* shows: spores (5)5.5—7 $\times$ (3)3.5—4 μm, ellipsoid to oblong, pale to bright rusty brown in Melzer's sol., wall thin, germ pore lacking; basidia 4-spored; brachybasidioles 8—12 μm in diam., reviving too poorly to measure accurately; cuticle of subglobose to globose cells 25—35 μm in diam. above a layer of elongate radial hyphae; clamp connections not seen.

Leucocoprinus brebissonii (Godey *in* Gillet) Locquin

Pileus 4—6.5 cm broad, ovate, becoming campanulate, umbonate, striate toward the margin; cuticle continuous at first and gray with a touch of lavender,

becoming diffracted into fibrillose-floccose scales, the scales closely spaced near the disc, progressively larger and more widely separated toward the margin, avellaneous, surface between the scales minutely fibrillose, white becoming tinted with avellaneous. Flesh thin, 2 mm near the stipe, unchanging when cut; odor and taste not recorded.

Lamellae approximate, white, close, subventricose, 5 mm at broadest point.

Stipe 8—12.5 cm long, 4—6 mm thick at the apex, enlarged below to 7—8 mm thick at the base, minutely fibrillose, pallid, becoming tinged with avellaneous toward the base, turning brown where handled, hollow, the cavity with a silky lining but not stuffed, base covered with a white mycelium. Annulus membranous, superior, narrow (scarcely 2 mm), white above, avellaneous below, reddish-brown on the thick fibrillose-floccose edge, sometimes becoming free, sometimes fugacious.

Spores 9—12 X 7—9 μm, oval with a truncate apex with a distinct germ pore, reddish-brown in Melzer's sol. Basidia extending out of the hymenium only a short distance when sporulating, the pedicel when present short. Brachybasidioles poorly differentiated, ±broadly fusoid. Pleurocystidia not seen. Cheilocystidia 30—60 μm long, 8—20 μm at widest point, clavate to fusoid-ventricose with a pointed apex or fusoid-ventricose with a neck 3—4 μm thick. Cuticle of the disc and scales of pileocystidia 40—70 X 3.5—9(—12) μm, slender, elongate, cylindric, fusoid or somewhat ventricose or of undifferentiated hyphal tips. Clamp connections not seen.

Growing on leaf mold in a greenhouse, southern California, in August and in a greenhouse and outdoors in Oregon in the fall. This species has not been found in Michigan but is widespread in Europe.

The description of the macroscopic characters is based on P. M. Rea's notes on his no. 1122 at the University of Michigan Herbarium. The microscopic characters were taken from the same collection. Rea commented on the developing fruiting bodies as follows: "The unexpanded plants, observed two days before collecting, had the pileus and stipe most beautifully and copiously beaded with drops of a watery secretion, tasteless and not appreciably viscid which became slightly amber-tinted in drying. These were also present on pileus and stipe of the mature plants but less abundant."

Dried specimens have a characteristic appearance and would not be easily confused with any of the other species included here. The dried pileus is a dingy-tan with a distinct brown disc and distinct brown scales, the lamellae are dark brown, and there is considerable pallid mycelium at the base of the stipe.

Leucocoprinus cepastipes (Sow. *ex* Fr.) Pat.

Pileus 2—8 cm broad, fragile, very thin, cylindric to ovoid, becoming broadly convex to plano-convex, margin entire at first, becoming striate, striate-rimose, or plicate-striate to sulcate; disc truncate when young, sometimes umbonate later; surface of the disc continuous, glabrous to finely tomentose,

elsewhere the surface covered with finely mealy to fibrillose scales; pale grayish-brown to whitish or white at first (sometimes the disc but not the scales brownish), becoming dingy-white then tinged pale-tan to pale yellowish-brown in ageing. Flesh thin and fragile, remaining white or staining straw-yellow to light pinkish-cinnamon when bruised. Odor and taste not distinctive.

Lamellae remote from the stipe, crowded, thin, white becoming dingy, margin even, finely fimbriate under a lens.

Stipe 3—12 cm long, 2—6 mm at apex, enlarged downward and somewhat fusiform-ventricose to distinctly clavate toward the base and in some mature specimens terminating in a short point, glabrous to faintly pruinose above, more tomentose below, white at first, becoming delicately flesh-tinged to pale-brown, sometimes straw-yellow then light-brown after handling. Annulus rather large, superior, flaring, membranous with a lacerate margin, white to whitish, subpersistent to evanescent.

Spores (6.5)7—9(—10) × 6—7.5(—8) μm, broadly ovoid, thick-walled, yellowish-brown to rusty-brown in Melzer's sol., germ pore present (in some mounts abnormal ±rectangular spores present). Basidia 4-spored, clavate at first, elongating and protruding from the hymenium when sporulating, sometimes the base pedicel-like. Brachybasidioles difficult to see, 15—20 μm broad, saccate to broadly clavate. Pleurocystidia not seen. Cheilocystidia 30—50 × 10—17 μm, fusoid-ventricose, clavate, or saccate, sometimes mucronate or sometimes with a long, slender neck and pointed beak. Lamellar trama very loosely interwoven with large air spaces, oleiferous hyphae present. Pileus cuticle of pileocystidia 45—110 × (4)9—15 μm, obtuse at the apex and sometimes swollen at the base, these agglutinated into fascicles which may become partially repent; or the surface covered with simple hyphal end cells rounded at the tips, surface of disc on young specimens of appressed, somewhat contorted hyphae. Clamp connections not seen.

Growing in soil bins in the greenhouse at the University of Michigan, fruiting at irregular intervals. This species is fairly common in nature in southeastern Michigan. It is widely distributed in rich humus, compost, sawdust, etc.

When dried the lamellae are pale-tan, the surface of the pileus uniformly pale dingy-tan with the umbo only slightly to much darker-brown; well-defined dark colored scales are lacking.

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DISTRIBUTIONS OF SOME WESTERN NORTH AMERICAN PLANTS DISJUNCT IN THE GREAT LAKES REGION

Robert J. Marquis

Department of Botany, University of Iowa,
Iowa City 52242

Edward G. Voss

Herbarium, The University of Michigan,
Ann Arbor 48109

Certain plant species of major phytogeographic interest have long been known to occur in the Great Lakes region and also extensively in the central Rocky Mountains, the Cascades, the Sierra Nevada, the northern Coast Ranges, and/or other parts of western North America, but with no stations (except in some cases the Black Hills of South Dakota) between the west and the Great Lakes region. Here, they reappear in more or less localized distributions. Fernald (1925) published the first major collection of evidence concerning these plants, and later (1935) followed with a more detailed consideration relevant to the Great Lakes area after having explored from the Bruce Peninsula to the Keweenaw Peninsula for a few days early in the previous summer. His friends A. S. Pease and R. C. Bean had explored the north shore of Lake Superior in 1933.

Fernald (1935, p. 218) noted that "these recent short excursions of New Englanders about the Upper Great Lakes have yielded many species apparently little known or hitherto unreported in the region." This was at least a veiled implication of neglect of the local flora by local botanists! Although indeed many fine records were obtained by the "New Englanders," the situation was not really as bleak as their failure to examine local herbaria may have suggested;[1] and certainly now, nearly a half-century after Fernald's excursion into the area, there is far less evidence of neglect. Some of the "critical species" were shown from as few as one or two localities in the Great Lakes region on old maps, such as the classic ones of Fernald (1925, 1935), which are often copied. A principal aim of the present paper is to show how many localities most of these species in fact have—and, by contrast, to affirm the very local occurrence of others despite the great amount of field work in the Great Lakes region during the past 40–50 years.

Since the time of Fernald's pioneering work, there has been much discussion in the literature on the subject of western species disjunct in the Great Lakes region, and theories have been proposed to explain the phyto-

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[1]For one example, Fernald could "find no other record" of *Aster nemoralis* from Michigan when reporting his own from near Emerson, Chippewa Co.—exactly the same place from which C. K. Dodge had published a report 14 years previously, in a flora of Chippewa Co.

geographical problems that these distributions present (we shall comment on these in conclusion). But no comprehensive effort seems to have been made to define this floristic element: which species should be included on the basis of actual disjunction in the light of up-to-date knowledge; and (our major concern at this time) what the total range within the Great Lakes region is for each. Definitions are not easy, nor free of ambiguity, but we have selected 28 species for presentation as principal disjuncts in our area. Except for a few of extremely restricted occurrence, distribution maps for the Great Lakes region are provided for these, and published maps showing, at least in general terms, all or most of the North American distribution are cited.

CRITERIA FOR DISJUNCTION

The principal criterion as to whether a species is to be considered a "western disjunct" is obviously a distinct discontinuity in distribution between the region of the Great Lakes and the west. In some cases, this discontinuity is associated with absence of favorable habitats, but in the most interesting and significant cases, it is not: the species is apparently absent even from presumably suitable habitats. We are not considering species of western *affinity* (of which there are many; cf. Iltis 1965, pp. 149–150), but those with an actual major *disjunction*. Nevertheless, the line is difficult to draw and surely others would produce lists with more or fewer species.

The line is also difficult to draw between species more strictly of boreal or arctic-alpine affinity (with some continuity far to the north of our region) and those of western or "cordilleran" affinity (the "cordilleran" ones, in the narrow sense, being those of mountainous situations). This problem is even more acute in the liverworts, as indicated by the discussion and maps of Schuster (1958). Some of the species once considered "cordilleran" disjuncts around the Great Lakes are now known to be more or less continuous across the previously less well known regions of northern Canada. And some of the others may well represent merely the relics of such a distribution in the past. The effects of increased knowledge are nicely shown in published maps of the distribution of *Gentianella amarella*. In 1957, Gillett (Ann. Missouri Bot. Gard. 44: 252) showed a disjunction between northern Lake Superior and Manitoba, whereas in 1963 (Canada Dep. Agr. Publ. 1180: 70) the same author could "fill in" with several stations from western Hudson Bay into northern Manitoba—as might have been predicted, to be sure, from earlier known stations at similar latitudes east of Hudson Bay. *Osmorhiza depauperata*, often considered a disjunct like *O. chilensis*, does not display the same disjunction in the north. *Lonicera involucrata* is one of the species discussed and mapped by Raymond (1950, pp. 33–34), who observes—as had others before him—that many of the supposed disjuncts that occur in the region of the lower St. Lawrence are at best relics of boreal ranges and in many cases do yet occur in the area of James Bay and elsewhere in the far north. (Note, too, that not all of the species of cordilleran affinity listed and discussed by Raymond, pp. 109–112, are actually disjunct between the west and the Great Lakes, even if they are disjunct from the latter to Quebec.)

We have dealt with species, not with subspecies or varieties that in themselves might be disjunct taxa depending on the general acceptance and distinctness of the infraspecific variant. Some of these are mentioned, however, in supplementary remarks, such as *Pteridium aquilinum* var. *pubescens* and *Chimaphila umbellata* var. *occidentalis*. And we have not considered species with their principal range in the east but a disjunction in the west, e.g. *Myriophyllum farwellii,* recently discovered in British Columbia (Ceska & Warrington in Rhodora 78: 75—78. 1976). The species we consider here, then, have their major present distribution in the west and have a clearcut discontinuity with a range in the Great Lakes region (not connected, so far as we now know, in the north). In our region, these species occur entirely or almost entirely north of the Tension Zone of Wisconsin and Michigan, and most stations for them are rather closely associated with the borders of the Great Lakes—as can be readily seen from the maps. *Festuca scabrella* and *Agoseris glauca* both occur in several counties of the jack pine region of Michigan's north-central Lower Peninsula. Here, they are not at all associated with the lake shores and in addition there are far northern stations, some of which are clear on the maps by Hultén (1968). These and other species with assorted deviations from our basic pattern have—somewhat arbitrarily perhaps—been omitted from further consideration at this time.

Some of our western species show an additional disjunction to the Black Hills of South Dakota, which is a "steppingstone" of favorable habitat for them between areas farther west and the Great Lakes. McIntosh (1931, p. 172) noted:

> From a botanical standpoint the most important climatological difference between the Black Hills and the surrounding country lies in the fact that the Hills receive much more rainfall than the plains. It is chiefly by virtue of this greater precipitation that the Black Hills form an oasis in a relatively dry region, a forested island, as it were, in a sea of grasslands.

There are also a number of our western species which have a further disjunction in the lower St. Lawrence—Gaspé Peninsula region (along with, in some cases, northern New England, Labrador, and Newfoundland). But species with a very large range in the east have been excluded from our consideration.

In light of the above criteria, the disjunct species discussed below are placed into four categories based on their overall range in North America:

I. Species found in the west and the Great Lakes
 A. Those not disjunct in the Black Hills (either not occurring that far east in the western range, or if so, not disjunct there).
 B. Those with a disjunction in the Black Hills.
II. Species found in the west, the Great Lakes, and the St. Lawrence area
 A. Those not disjunct in the Black Hills (as above).
 B. Those with a disjunction in the Black Hills.

No two species have identical distributions, and definitions, as stated above, are arbitrary. Remarks with the discussions of the species call attention to some major variations in range, problems of interpretation, and additional species with intermediate degrees of disjunction and which might be considered by some to belong in the respective categories.

I. SPECIES OF THE WEST AND THE GREAT LAKES

A. WITHOUT A DISJUNCTION IN THE BLACK HILLS

1. *Agropyron spicatum* (Pursh) Scribner & J. G. Smith ⋮ Bluebunch Wheatgrass

Collected once in the Great Lakes region on bluffs in Keweenaw County, Michigan, by Farwell in 1895 (see Voss 1972, p. 161), this grass is characteristic of dry soils from Alaska and Yukon to California and New Mexico. It is in western South Dakota, but as its habitat would indicate, not disjunct to the Black Hills. The map by Hultén (1968, p. 184) shows two additional small areas in the Great Lakes region, probably based on published reports dependent on misidentifications.

2. *Chamaerhodos nuttallii* Rydb.

The first collection of this inconspicuous member of the Rosaceae in the Great Lakes region was made by Fernald and Pease in 1934, with Fernald (1935, p. 284) designating it as var. *keweenawensis*—a pilose variety endemic to West Bluff (Brockway Mountain) of the Keweenaw Peninsula. While the species has not been found elsewhere in the Great Lakes region, hairy plants resembling the alleged variety have been recognized in the main range of the species and its taxonomic significance is questionable (see Boivin in Nat. Canad. 87: 29. 1960). Geographically, however, our population is a very small, isolated one, and the species is designated "endangered" in Michigan. The principal range is more or less scattered from Alaska and Yukon to Colorado; eastward it ranges on dry hills and plains through southern Manitoba, North Dakota, northwestern South Dakota, and northwestern Minnesota. Its disjunction to the Keweenaw Peninsula is thus not as great as for many species, and it belongs in a category of Great Plains plants with a modest Great Lakes disjunction. Maps of its North American range are given by Fernald (1935, p. 214) and Hultén (1968, p. 624). The species is often included in *C. erecta* (L.) Bunge of eastern Asia.

3. *Crataegus douglasii* Lindley   Douglas Thornapple

This is a most distinctive hawthorn, with fruit dark blue-black when ripe. From southern Alaska it ranges through the Pacific Northwest and Montana south to northern California and through the Rocky Mountains, sparsely, to New Mexico. Old reports as far east as Manitoba and the Dakotas are questioned or disregarded by recent authors. This is thus a typical cordilleran disjunct, occurring with us in mixed forest and dry open spots, including rocky open woods and bluffs; it grows at the summit of the glacially deposited bluff above Lake Superior at the Grand Sable Dunes in Alger County, Michigan. The only locality in the Lower Peninsula of Michigan is Thunder Bay Island, Alpena County (C. F. Wheeler in 1895, MSC). In addition to a 1936 Bruce Peninsula collection (Krotkov 10624, TRT, det. J. B. Phipps), there are two by Joseph W. Johnson in 1974, reported to us by James S. Pringle; the Manitoulin Island record is based on two 1932 collections from Wekwemikongsing: Grassl 2260 (MICH, det. E. P. Kruschke, Phipps) & Koelz 4280 (MICH, det. Phipps). Hultén (1968, p. 600) maps the range in North America; more detail (although quite incomplete in the Great Lakes region) is given by Little (1976, map 59). Plants of
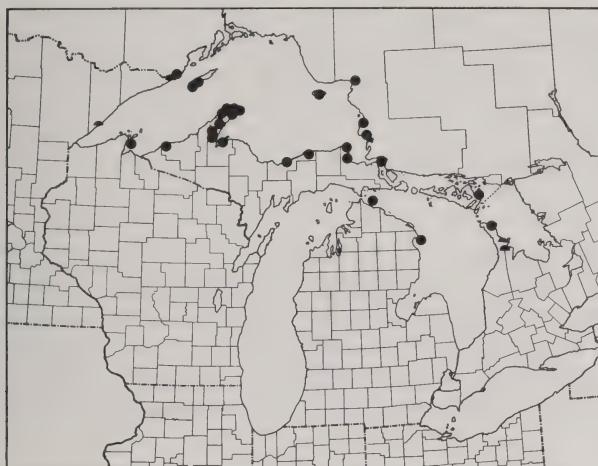
Great Lakes distribution of
3. *Crataegus douglasii.*

Michigan and Ontario were named by Sargent (Trees & Shrubs 2: 245. 1913) as *C. brockwayae,* honoring (at his request) O. A. Farwell's mother, Charlotte Louise Brockway.

4. *Cryptogramma crispa* (L.) R. Br.   Parsley Fern

Basically a circumpolar species, of which we have var. *acrostichoides* (R. Br.) Clarke in North America, this is not as clearcut a disjunct as many others. Very local in the Great Lakes area (some maps notwithstanding), it is frequent only on the northeastern part of the main island at Isle Royale, where it grows in crevices of dry rocks. The only Minnesota collection was made in Cook County in 1870 (J. C. Jones, MICH—see Voss 1978, p. 55), and there is an old collection from near Schreiber, Ontario (Reznicek, pers. comm.). From western-most Ontario and southeastern Manitoba, the species ranges, discontinuously,

Great Lakes distribution of
4. *Cryptogramma crispa.*

to Alaska, and in the west it grows (chiefly in the mountains) south to Mexico. Hultén (1968, p. 44) and Fernald (1935, p. 245) provide maps. Soper (Am. Fern Jour. 53: 120. 1963) has effectively disposed of an old report from Manitoulin Island, presumably the basis for "ids. of L. Huron" in Fernald (1950) and the similar range on some maps; reports from the Labrador-Quebec area seem also spurious (see Boivin 1967, p. 264; Scoggan 1978, p. 158).

5. *Disporum hookeri* (Torrey) Nicholson   Fairy Bells
   This species has been collected only once in the Great Lakes region, a specimen of var. *oreganum* (S. Watson) Q. Jones having been found in woods at Porcupine Mountains State Park, Michigan, in 1968 by P. W. Thompson (see Voss 1972, p. 416). A native of forests in the Pacific Northwest, east to Alberta, it has not been rediscovered in Michigan, where its occurrence is something of a mystery.
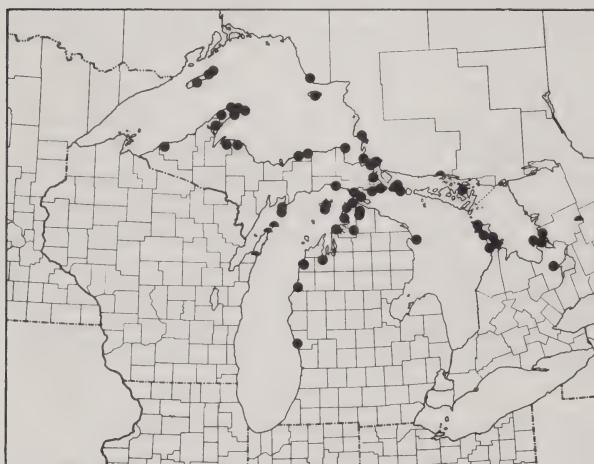
Great Lakes distribution of 6. *Festuca occidentalis.*

6. *Festuca occidentalis* Hooker   Western Fescue
   This grass, characteristic of open, often rocky or sandy woods and wooded dunes in the Great Lakes area, has a distribution which can be considered archetypical of a western species disjunct from the cordilleran region of North America. From the Pacific Northwest (British Columbia to central California) it ranges only as far east as southwestern Alberta, western Montana, and north-western Wyoming—whence it skips to Isle Royale and the Porcupine Mountains of Michigan. In the west it frequents dry sandy, gravelly, or rocky soils, conifer-ous woods, and the borders of forests and streambanks—not unlike its habitats here.

7. *Oplopanax horridus* (Sm.) Miq.[2]   Devil's Club

The devil's club grows in moist woods from southern Alaska, southwestern Yukon, and central Alberta south to Oregon and northwestern Montana. This awesomely spiny plant, well deserving of its common name, is then spectacularly disjunct to a very small area on Lake Superior, where it was first reported from Isle Royale in 1901 (W. A. Wheeler in Minnesota Bot. Stud. 2: 620). It is now known to occur at Isle Royale in wooded rocky hollows and shaded moist ravines at the northeast end of the main island (Blake Point) and on Passage, North Government, South Government, Edwards, Porter, and Smithwick islands (at all of which sites one of us [EGV] has seen—but not necessarily collected—it) and it is reported from others, including the Gull Islands near the International Boundary. Just off the Sibley Peninsula of Ontario, it is known from Porphyry Island. Small maps of its general distribution have been published by Fernald (1925, p. 251) and Hultén (1968, p. 696).

Great Lakes distribution of 7. *Oplopanax horridus.*

Several additional taxa could be included in this group, although with various doubts. *Antennaria rosea* Greene is a composite with a striking rosy colored involucre, belonging to a complex group that makes us hesitate to say anything of its distribution. Hyypio (1952) reported it from the Great Lakes region: two collections from Isle Royale and one from Fort William (Thunder Bay). The overall range in the west is from Alaska south to California and New Mexico and east to northern Manitoba. However, it is also in the James Bay

[2]The International Code of Botanical Nomenclature (Rec. 75A.2b) recommends that all generic names ending in -*panax,* including *Oplopanax,* be treated as masculine, and the epithet should therefore not be written *horridum* as is sometimes done.

region and is mentioned by Scoggan (1979, p. 1468) from northern Labrador. So it is perhaps as much a boreal disjunct as it is a cordilleran one. It is "on dry or grassy hillsides over the state" of South Dakota according to Van Bruggen (1976) and is in the Black Hills according to McIntosh (1931) and Thilenius (1971) but not Dorn (1977). *Carex praegracilis* W. Boott appears to be disjunct from the grasslands of western Minnesota to northern Michigan, where it was found at two places: near Manistique in 1915 and near Eagle Harbor as early as 1934 (see Voss 1972, p. 256). Fernald (1935, p. 253) considered his Eagle Harbor colony as "certainly indigenous." Hermann (Man. Caric. Rocky Mts., U. S. Dep. Agr. Handb. 374: 62. 1970) considers the species to be native from Manitoba, Iowa, and Kansas westward to the Yukon, British Columbia, California, and Mexico, "and adventive eastward." There may be some question concerning its status in northern Michigan; certainly it is aggressively adventive now along highways in southern Michigan and Ontario, and perhaps in northern Illinois (see Reznicek in Mich. Bot. 19: 27. 1980).

Chimaphila umbellata var. *occidentalis* (Rydb.) Blake was considered a western disjunct by Fernald (1935, pp. 324–325), based on northern Michigan collections, but it is very close to the common eastern var. *cisatlantica* Blake and its significance is doubtful. *Equisetum telmateia* Ehrh., the giant horsetail, is a species (represented by var. *braunii* (Milde) Milde in North America) occurring along the Pacific Coast from Alaska to southern California. Farwell collected it in Keweenaw County, Michigan, in 1890 and 1895 (if the labels be trusted) and there are early reports from New York. These are regarded with suspicion, but not outright rejection, by Hauke (Nova Hedwigia 30: 434–435. 1978). Farwell (Rep. Mich. Acad. 6: 302. 1905) stated the plant to be very rare in Keweenaw County and described the situation realistically: "I know of but one place where it is to be found. This is in an alder thicket and the ground is generally moist and of a rich muck. The sterile fronds in summer are often three feet high and have a spread of branches often measuring two feet." Later (Am. Fern Jour. 27: 7. 1937) he merely said "I have not been to the station since and do not know if it is still there." Apparently it aroused no phytogeographical curiosity on his part, and no one who has searched for it since has been able to relocate it.

Malaxis paludosa (L.) Sw., the bog adder's-mouth, is a very rare bog orchid known from the Great Lakes only on the Sibley Peninsula of Ontario. It is also known from the Hudson Bay Lowlands (Baldwin in Canad. Field-Nat. 75: 74–77. 1961) and northern Minnesota (Clearwater & Ottertail cos.). The tiny plants are so very inconspicuous that the species may well be more widespread than is now documented, as mapped by Luer (1975, p. 302) from Lake Superior northwest to Alaska. Rather than being a major disjunct in our region, it seems to be a rare and erratic boreal relic. *Potentilla hippiana* Lehmann is a native of western North America, occurring east to southern Manitoba. It has been collected at two sites in the Lake Superior region: roadsides at the Whiting Shaft Location near Calumet, in Houghton County, Michigan (Farwell 11713 in 1937, BLH, det. Fernald—see Rhodora 40: 135. 1938) and Silver Islet, at the end of the Sibley Peninsula, Thunder Bay District, Ontario (stoney ridge, Garton 1219 in 1950, MSC, CAN—see Phytologia 4: 90. 1952; Perry's Bay, Löve & Löve

6918 in 1955, CAN; vicinity of old jail, Garton 16526b in 1975, MICH, CAN). These situations strongly suggest that the species is introduced here, as it is reported in Quebec (Cayouette 1966). The status of the closely related and variable *P. gracilis* eastward may be similar.

Solidago decumbens var. *oreophila* (Rydb.) Fern. is stated by Fernald (1950, p. 1396) to occur in northern Michigan in addition to the west (Yukon to New Mexico). The basis for this is presumably a collection from Lookout Mountain, Keweenaw County (Fernald & Pease 3544 in 1934, MICH). This variety is "embarrassingly transitional" to the typical one (Fernald in Rhodora 38: 203. 1936) and Cronquist (in Gleason 1952, 3: 418) considers *S. decumbens* to be the same as typical *S. spathulata*, which is approached by occasional plants in our range, where supposedly only ssp. *randii* occurs. In view of the dubious significance of *S. decumbens* in relation to the abundant and variable *S. spathulata* in this region, we do no more than mention it.

B. WITH A DISJUNCTION IN THE BLACK HILLS

8. *Adenocaulon bicolor* Hooker   Trail Plant
     This composite, with its distinctive triangular green leaves, white-woolly beneath, and glandular achenes, is characteristic of moist shady woods from
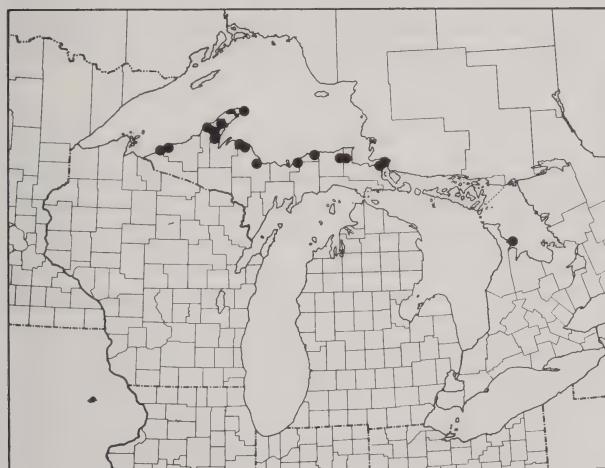
Great Lakes distribution of 8. *Adenocaulon bicolor.*

southern British Columbia and southwestern Alberta south in the mountains to central California and northwestern Montana. It is then widely disjunct to the Black Hills and the Great Lakes region, primarily the northern part of the Upper Peninsula of Michigan, where it is not rare along rocky streams, in ravines and on banks in moist hemlock-hardwood forests. It was collected on Cape Croker in the Bruce Peninsula in 1895 but is now assumed to be extinct

there. Statements and maps indicating it in northeastern Minnesota cannot be verified. The genus is also found in South America, a geographic feature shared with *Osmorhiza* among our western disjuncts. Fernald (1935, pp. 212–213) has mapped the world and North American distributions.

9. *Arnica cordifolia* Hooker   Heart-leaved Arnica

Fernald (1935, pp. 334–337) named the eastern representative of this species *A. whitneyi,* in honor of W. D. Whitney, who discovered it at Copper Harbor, Michigan, in 1849 (see also Voss 1978, pp. 27–28). Usually, however, it is now merged with or considered a variety or subspecies of *A. cordifolia,* a widespread cordilleran species with large showy yellow heads, found in woods and meadows from Alaska south in the mountains to California, Arizona, and New Mexico, as well as in the Black Hills and in the Riding Mountains of Manitoba (White & Johnson 1980). The eastern endemic subspecies (or very closely related species) is designated as "endangered" in Michigan, being known only from a very limited portion of Keweenaw County, from Copper Harbor to Eagle Harbor (a distance of about 14 miles), where it is found in open woods and rocky bluffs. The only other locality for it is in balsam woods over boulders at Ravine Lake on the Sibley Peninsula, Ontario (Garton 15486 in 1973, MICH; 18959 in 1979, MICH). In his monograph of the genus, Maguire (1943) correctly stated that it is known from "a restricted area," the collections "all from Keweenaw County," but his map (p. 450) is wholly erroneous, showing the subspecies at five localities in the eastern Upper Peninsula, 100–200 miles from the type (and only) locality in the state—where he does not show it. Evidently these errors were incorporated in the map by Hultén (1968, p. 918), but these maps nevertheless emphasize the disjunction.

10. *Ceanothus sanguineus* Pursh   Redstem Ceanothus

This species of "wild-lilac," a tall shrub often with characteristic reddish purple branches, was first collected in Michigan by Farwell in 1886, near Copper Harbor. Late in 1914 he rediscovered the species (Rep. Mich. Acad. 17: 171–172. 1917) and the next year (Farwell 1915) he determined it to be locally plentiful—as it is to this day along the borders of woods and bluffs in northern Keweenaw County, but nowhere else in the Great Lakes region. In the northwest, it is found in similar partly cut-over or partly shaded habitats from southern British Columbia to northwestern Montana, south to California, also (?) occurring in the Black Hills. Fernald (1935, p. 210) maps it in the Black Hills, and it is often said to occur there; Thilenius (1971) added it to McIntosh's 1931 list, but it is not in the Black Hills according to Dorn (1977), nor is it listed for South Dakota by Van Bruggen (1976). Good illustrations and some information on ecology of the species are provided by Hickey and Leege (1970), whose map of regions in which it is present is extremely misleading, showing a region throughout the Lower Peninsula of Michigan eastward to central New York—but omitting the only area where it *is* found.

11. *Melica smithii* (Gray) Vasey

This is one of the very few cordilleran species for which the type locality is in the Great Lakes area (in this case, Sault Ste. Marie, Michigan) rather than

in the west. The original description also cited Isle Royale, but no specimens from there have been located. It is characteristic of deciduous woods, especially rich beech-maple stands and wooded dunes in the northern Great Lakes region, found across much of the Upper Peninsula of Michigan and the northwestern Lower Peninsula; at one site south of Mellen in Ashland County, Wisconsin (Read 1976 & pers. comm.); and rather common in damp rich woods throughout the Bruce Peninsula (Krotkov 1940) as well as southward (Dore & McNeill 1980). It has also been collected in Gatineau Park, Quebec, about 10 miles north of Ottawa (Dore, pers. comm.). As mapped sketchily by Fernald (1935, p. 217), the range of this species in the west, where it is also a plant of moist woods, is from southern British Columbia and southwestern Alberta south to Oregon and Wyoming, with a distinct disjunction in the Black Hills.
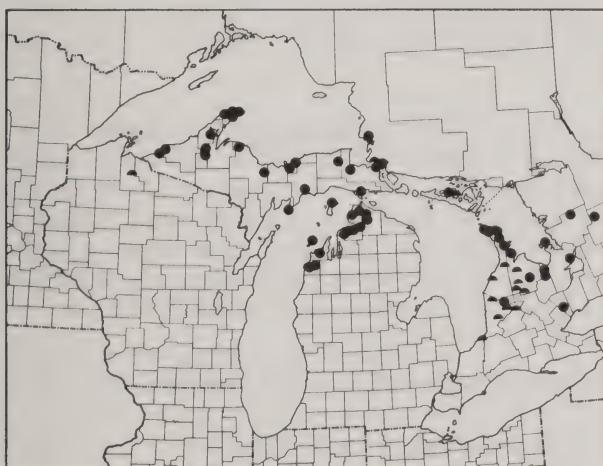
Great Lakes distribution of 11. *Melica smithii*.

### 12. *Rubus parviflorus* Nutt.   Thimbleberry

This is another species with the type locality in our area (Mackinac Island—see Voss 1978, p. 5). It is one of the most widely distributed of the western disjuncts, occurring from the Bruce Peninsula across northern Michigan and around Lake Superior to the Arrowhead region of Minnesota. It is especially abundant at places near Lake Superior, such as Isle Royale, the Keweenaw Peninsula, and the Porcupine Mountains in Michigan, and its large red highly edible fruit follows a large white flower. Likewise widespread in a diversity of wooded to open areas and borders of woods in the west, it occurs from southern Alaska to northern Mexico, in addition to the Black Hills. Maps of minor variants, most of which are also disjunct to the Great Lakes, are given by Fernald (1935, pp. 277–284); the overall range is indicated by Fassett (1941, p. 359).

13. *Vaccinium membranaceum* Britton   Bilberry

With large purple-black juicy fruits to 18 mm in diameter, this is another choice edible plant along the Michigan shore of Lake Superior, apparently the
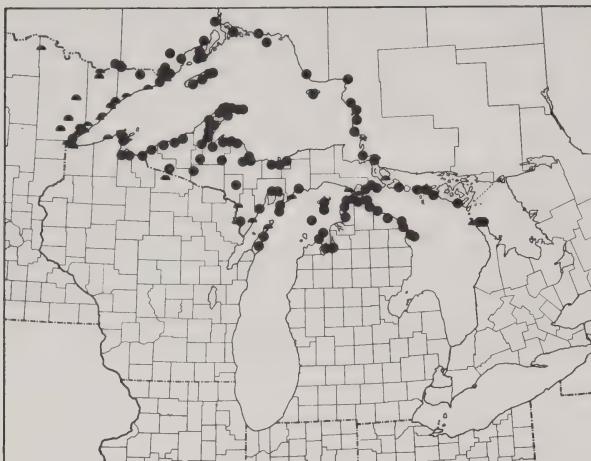
Great Lakes distribution of
12. *Rubus parviflorus.*

only area in which it occurs in eastern North America. (Old reports from the
Bruce Peninsula are unverified.) In Michigan, it is a shrub of woods, usually
coniferous, including edges on stable dunes. From southeastern Alaska, British
Columbia, and Alberta, it ranges south to California and Montana (farther if
V. globulare is included). Dorn (1977) could not confirm its presence in the
Black Hills, but Van Bruggen (1976) says it is "very rare" there. Fernald (1935,
p. 211) and Hultén (1968, p. 732) map the overall range in North America.

II. SPECIES OF THE WEST, THE GREAT LAKES, AND THE ST. LAWRENCE

A. WITHOUT A DISJUNCTION IN THE BLACK HILLS

14. *Arabis holboellii* Hornem.
        Although often considered a classical disjunct species in the Great Lakes
region, *A. holboellii* displays less dramatic gaps in its range than most of the
others considered here, and its inclusion could be questioned. It is a good exam-
ple of a boreal/cordilleran mixture. Fernald (1950, p. 728) implies no disjunc-
tion from Quebec to Ontario and Michigan in the range of var. *retrofracta*
(Graham) Rybd. (which is the principal if not only variant in our region)—and
there are collections from Algonquin Park and near Kingston, Ontario; whereas
Hultén, on the contrary, maps a disjunction between those regions but not west
of the Great Lakes. In fact, the species occurs in northeastern Minnesota and
adjacent Ontario and then appears to be absent until the northwest corner of
Minnesota and western Ontario. Although found in the Black Hills, it is not
isolated there. The species also occurs in Greenland (not var. *retrofracta*), al-
though not in the Canadian arctic. Hopkins (1937, p. 183) referred to *A.
retrofracta* as "a cordilleran species found eastward only in isolated and ex-
tremely local stations in northern Michigan, extending throughout the Rocky
Mountains and Pacific coast regions," and he mapped its range (p. 180). This is

Great Lakes distribution of 13. *Vaccinium membranaceum.*

now considered a variety of *A. holboellii,* and is known from Quebec (see Rollins in Rhodora 43: 440–441. 1943), as well as other stations not known to Hopkins. The other, less common varieties of the species do not significantly alter the total range, as mapped by Hultén (1968, p. 549). The habitat of *A. holboellii* around the Great Lakes is typically open rocky and gravelly bluffs and dry sandy soils including low dunes.

15. *Arenaria macrophylla* Hooker　　　　　　　　　Bigleaf Sandwort
　　　Disjunct from the Cascades and the Rocky Mountains, ranging from British Columbia to California and New Mexico, this species in the Great Lakes region may have a wider distribution than is presently known because of its in-
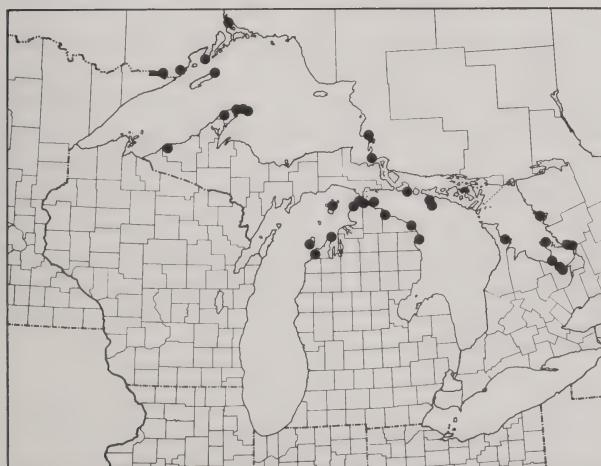
Great Lakes distribution of 14. *Arabis holboellii.*

conspicuous nature and superficial resemblance to other small Caryophyllaceae. Its puberulent stems, eciliate leaves, and conspicuous uncleft petals will distinguish it, for example, from *Stellaria calycantha,* with which it is sometimes confused. The habitat in our region is bluffs and rock outcrops, often in open woods. In the east, the species occurs in New England and the Gaspé area. It is also in northern Quebec and Labrador, as well as in northern Saskatchewan and the Great Slave Lake area in the west, so that it is a boreal species with large disjunctions. The maps of Fernald (1925, p. 259) and Porsild (1958, map 18), taken together, give a general picture of its range, though showing only the north shore of Lake Superior in the Great Lakes.
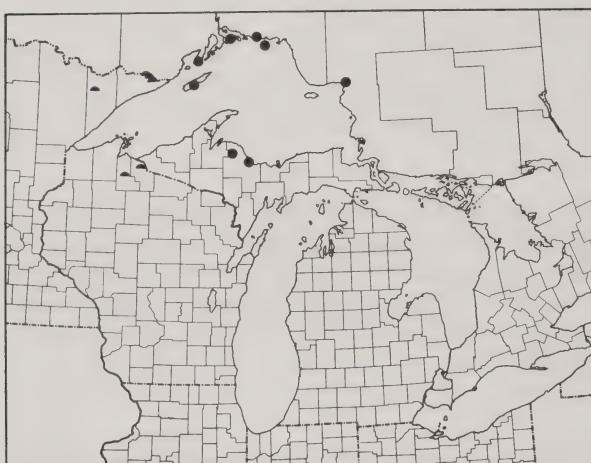
Great Lakes distribution of 15. *Arenaria macrophylla.*

16. *Dryas drummondii* Richardson   Yellow Mountain-avens

     This distinctive member of a difficult arctic-alpine genus is an excellent example of this disjunct pattern. It undoubtedly represents the relics of an earlier, colder postglacial climate, and is simply more restricted in range than *D. integrifolia,* of similar affinity. *D. drummondii* occurs in the west from the Mackenzie District to Alaska, south to Montana and Oregon. It is found on calcareous cliffs, talus, and gravel bars. In the Lake Superior region it is known only from conglomerate shore rocks of the Slate Islands and from Michipicoten Island. There is a specimen (Whelan 135 in 1937, TRT) labeled as collected at Smoky Falls, Cochrane District, Ontario. In the east, it occurs around the Gulf of the St. Lawrence, including Gaspé and western Newfoundland (also Lake Mistassini, fide Scoggan 1978, p. 915). Maps have been published by Hultén (1968, p. 629), Porsild (1958, map 18; Canad. Field-Nat. 61: 193. 1947), Miller and Thompson (1979, p. 205), and others.

17. *Galium kamtschaticum* Steller   Boreal Bedstraw

     This coniferous forest species was collected in Ontario on the east side of Lake Superior in 1935 (Taylor 1938, p. 130). It is strikingly disjunct from the

Great Lakes distribution of
16. *Dryas drummondii.*

Pacific coast, where it ranges from Alaska to Washington. It also occurs from northern New York to Quebec and Newfoundland. Maps of the North American range have been published by Hultén (1968, p. 839) and Porsild (1958, map 18).

18. *Mimulus moschatus* Douglas					Muskflower
     The important question with this species is whether it is truly native in the Great Lakes region or an introduction. Farwell, a long-time resident of the Keweenaw Peninsula, wrote (1915) that "so far as I have been able to learn, it was never cultivated in the Copper district of Michigan unless gathered for the purpose from the local native plant." Its sporadic occurrences in eastern North America suggest that at least some of its stations represent introductions, as suspected by Pennell (1935, p. 115), who considered the species native in at

Great Lakes distribution of
18. *Mimulus moschatus.*

least northern Michigan, Quebec, and Newfoundland. Fernald (1950, p. 1275) held a similar opinion. A frequenter of moist places, it is found in roadside ditches and hardwood forest openings, along stream banks and swamp borders— likely habitats for a "weed." Its distribution in western North America is from British Columbia southward, primarily in the mountains, but apparently no map of its range has been published.

19. *Poa canbyi* (Scribner) Piper

Collected on Isle Royale at Monument Rock, a wave-cut stack (of volcanic rock) associated with the shoreline of postglacial Lake Minong (ca. 10,500 years ago) (McFarlin 2175 in 1930, MICH; Voss 14749 in 1975, MICH, MSC, GH, US). Reported from the Lake Superior region of Ontario by Argus and White (1977, p. 39); more detail (and some doubt about Pigeon River material) concerning Ontario records is in Dore and McNeill (1980, p. 138). Determining the overall range of the species is difficult. Manuals cite Minnesota, but it is apparently not in the Lake Superior region of that state (Butters & Abbe 1953; Lakela 1965). Hultén's map (1968, p. 142) shows a very large disjunction to the Great Lakes area but apparently none to the Black Hills. Dorn (1977) does not include it in the Black Hills, but Thilenius (1971) added it to McIntosh's list of 1931; according to Van Bruggen (1976) it is in western South Dakota. From there, it ranges, intermittently, to Alaska, northern California, and Colorado. It appears again in eastern Quebec, including Gaspé. Porsild (Natl. Mus. Canada Bull. 216: 68. 1966) gives a good map of its Canadian range (plus Isle Royale), which reveals the great disjunctions to the eastern areas.

20. *Polygonum douglasii* Greene   Douglas' Knotweed

Although occurring in northern Minnesota and adjacent Ontario from Lake of the Woods east to Lake Superior, this species seems to be disjunct in the United States from there to the Black Hills—the only region from which it is reported in South Dakota. But scattered reports from southern Manitoba cast
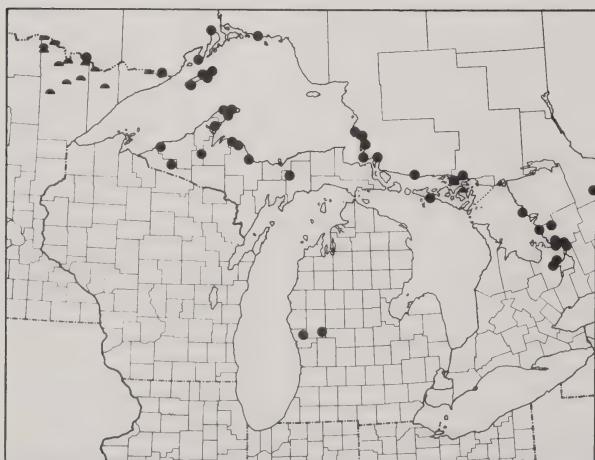
Great Lakes distribution of
20. *Polygonum douglasii*.

some doubt on whether this should be included as a truly disjunct species. Its affinity for dry sandy habitats makes difficult any determination as to whether the species is indigenous at the sites where it has been collected in sandy soil in west-central Michigan—and perhaps elsewhere. In this respect, its range presents problems similar to those for *Mimulus moschatus*. It occurs near the eastern end of Lake Ontario, in New York and Ontario, and ranges south in eastern New York nearly to the mouth of the Hudson River (Mitchell in N. Y. St. Mus. Bull. 431: 32. [1978]). Its distribution northward in New England to Quebec thus gives it a wider range in this part of the continent than those species restricted closer to the lower St. Lawrence. Most of the other disjunct species whose common habitat in the Great Lakes region is rocky and sandy areas are much less widespread. In the west, this distinctive knotweed with strongly reflexed flowers and fruits ranges from British Columbia to Manitoba, south to California and New Mexico. No map of its range seems to have been published.
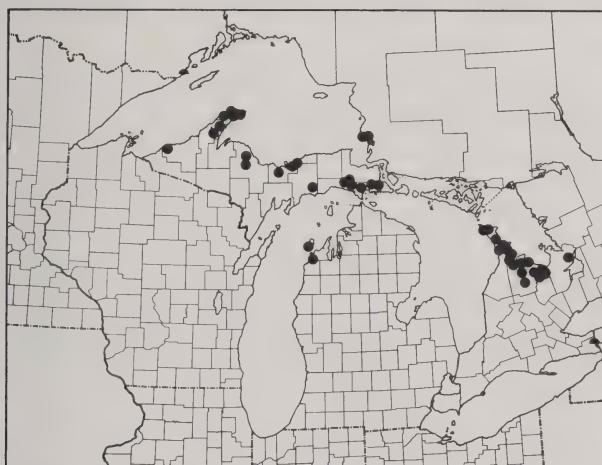
Great Lakes distribution of
21. *Polystichum lonchitis.*

21. *Polystichum lonchitis* (L.) Roth   Holly Fern
    A circumpolar species primarily of calcareous shaded habitats, with us often associated with rocks of the Niagara Escarpment. It is common in the woods of the Bruce Peninsula, ranging around Georgian Bay and the Niagara region of Ontario. It appears again in the area of Nova Scotia, Newfoundland, and Gaspé. In the west it is found from the Aleutians, southern Alaska, and Yukon south to northern California and (at least) Utah. Maps have been published by Fernald (1935, p. 207), Hultén (1968, p. 53), and Roland (Proc. Nova Scot. Inst. Sci. 20: 87. 1941).

22. *Pterospora andromedea* Nutt.   Pine-drops
    This species is frequently cited as illustrating an east-west disjunction. It is characteristic in the Great Lakes region of dry pineland or sometimes moister woods and is considered saprophytic, i. e. dependent upon a fungus for its nutri-

tion; presumably that fungus is in turn mycorrhizal with the roots of trees (e. g. conifers), as in the case of *Monotropa* (see Campbell in Mich. Bot. 10: 63–66. 1971), but no demonstration of the three-way relationship seems to have been made for *Pterospora.* The species is unknown from the pinelands of northern Wisconsin and Minnesota, with a large disjunction between the Black Hills and Lake Michigan. From the latter region, it ranges eastward, sparsely, through Ontario to Quebec. Compared with most of our cordilleran species, it is not as disjunct to the lower St. Lawrence, where it has been found only as far east as Bic (almost to Gaspé), as well as on Prince Edward Island. A map of its range in Ontario and adjacent Quebec is given by Gillett (1972); additional localities are on Manitoulin Island [Gore Bay (Grassl 2267 in 1932, MICH) and Meldrum Point (Grassl 2266 in 1932, MICH)] and the Bruce Peninsula, where it is said to be very rare (Fed. Ontario Nat. 1969, p. 44—not mapped). Many of the records from the eastern range of the species are very old. In the west, it ranges (as mapped by Bakshi, 1959) from British Columbia (also ?Alaska) and southwestern Sasketchewan south, primarily in the mountains (and including the Black Hills), into Mexico.
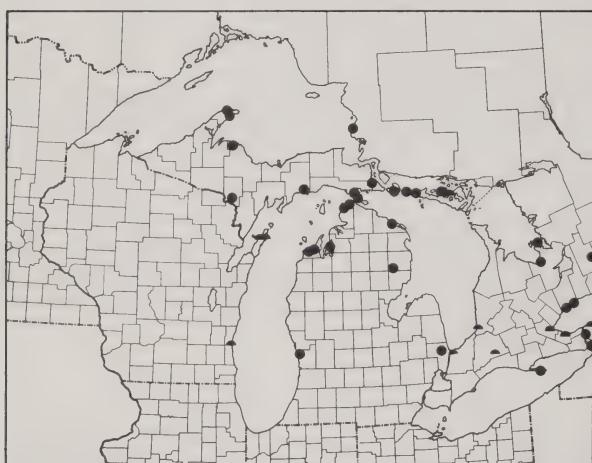

Great Lakes distribution of 22. *Pterospora andromedea.*

23. *Vaccinium ovalifolium* Sm.   Bilberry

Vegetatively, this species is distinguished from *V. membranaceum* (with which it frequently grows in northern Michigan) by its paler leaves, entire or nearly so. The fruit in both species lacks the "crown" formed by the persistent calyx of our common blueberries; in *V. ovalifolium,* the ripe fruit is blue as the result of a pale waxy bloom. Found along the Pacific coast from Alaska and southwestern Yukon to Oregon and western Montana, it reappears in habitats of steep wooded slopes, hemlock-hardwoods, and wooded, sometimes open, dunes from the Keweenaw Peninsula of Michigan to the Algoma District of Ontario, north to Davieaux Island on the south side of Michipicoten Island

Great Lakes distribution of 23. *Vaccinium ovalifolium.*

(Garton et al. 14576 in 1976, MICH, CAN). With another break in its distribution, it is found again around the mouth of the St. Lawrence (Laurentide Park to Newfoundland and Cape Breton Island). Argus and White (1977, p. 48), perhaps after Boivin (1967, p. 418), indicate a continuous distribution from Lake Superior to Quebec, but we know of no evidence for this. The disjunctions are shown nicely on maps by Fernald (1925, p. 253), Hultén (1968, p. 733), and Raymond (1950, p. 12). (Raymond, p. 110, includes *V. ovalifolium* in a list of species with a series of known subarctic or arctic stations forming a trans-Canadian connection between the St. Lawrence and cordilleran regions, but this is not supported by his own map nor his listing of the species on the previous page as a disjunct. *V. ovalifolium* may indeed have had a history similar to that of *Lonicera involucrata* and other species with intermediate subarctic stations, but its present known distribution is apparently otherwise.)

A species of dubious status which would belong in this group if truly part of our flora is *Cheilanthes siliquosa* Maxon (also called *Pellaea densa*, *Aspidotis densa*, and other names), one of the lip ferns. It is known from serpentine areas in Gaspé and Megantic counties, Quebec, but the only record from the Great Lakes region is nearly a century old, from Durham, Gray County, Ontario (well south of the Bruce Peninsula). It is sometimes merely assumed to be extinct there (Stebbins 1935, p. 67; Scoggan 1978, p. 158), but in the absence of suitable habitat and any further collections despite thorough searching (cf. Morris & Eames, Our Wild Orchids, p. 315. 1929), an error in labeling may be suspected and most recent authors appear inclined to discount the alleged Ontario occurrence (Boivin 1967; Argus & White 1977; Mickel, How to Know the Ferns and Fern Allies, 1979). In the west, the species ranges from the Pacific Northwest to Montana (with reports from New Mexico and Utah). Another taxon which might be included with this group is *Epilobium paniculatum* Nutt., which consists of both introduced and indigenous varieties in

eastern North America. Plants of the latter are "apparently native" in western Quebec and the Bruce Peninsula (Gleason 1952, 3: 587) or introduced there (Scoggan 1979, p. 1136) as well as occurring through a wide area in western North America. However, the species (presumably the typical variety native only in the west) is spreading in Ontario, Michigan, and Wisconsin. Both varieties have more or less weedy habits and possibly neither is really native in the east.

B. WITH A DISJUNCTION IN THE BLACK HILLS

24. *Arnica lonchophylla* Greene   Arnica

Maguire (1943) recognizes three subspecies, associated with the major disjunct areas: subsp. *lonchophylla* ("genuina") on "gravelly open slopes" from Alaska to northern Manitoba; subsp. *arnoglossa* (Greene) Maguire in the Black Hills (also Big Horn Mountains of Wyoming) and northeastern Minnesota; and subsp. *chionopappa* (Fern.) Maguire from Gaspé to Newfoundland. Butters and Abbe (1953, p. 200) identify their *Arnica,* however, as *chionopappa,* locally abundant on a north-facing cliff of calcareous slate at Clearwater Lake. Lakela (1965, p. 392) similarly refers her collections from adjacent Lake County. Argus and White (1977, p. 14) consider the range more or less continuous from western Ontario to southern Quebec and Boivin (1967, p. 1049) cites it from New Brunswick to Alberta, but the maps of Hultén (1968, p. 922) and Maguire (1943, p. 429) and the statement by Scoggan (1979, p. 1476) all suggest more disjunction. Nevertheless, the species as a whole is doubtless one of northern affinity, the relic southern disjunct populations having evolved some differences in their isolation. Ediger and Barkley (N. Am. Fl. II, 10: 32–33. 1978) do not recognize infraspecific taxa, but indicate that part of the range is from northeastern Minnesota "to the vicinity of James Bay."

25. *Collinsia parviflora* Lindley   Small-flowered Blue-eyed-Mary; Blue Lips

This small blue-flowered annual, possibly overlooked by collectors, grows in moist places and gravelly or rocky bluffs from southern Alaska and adjacent Yukon to California and Colorado. Its only area in South Dakota is the Black Hills, but it is widely scattered in Saskatchewan and is in southeastern Manitoba, reappearing in northern Michigan and adjacent Ontario. We include it tentatively in this grouping on the basis of stations in eastern Ontario and western Vermont. However, this is an annual, often in rather sterile soil eastward, and as for *Polygonum douglasii,* one might question whether it has been indigenous at all of the eastern stations. The recent collection in Schoolcraft County, Michigan, near Lake Michigan (Gillis 2455 in 1958, MSC) is from "weedy sand barrens" where it may well be adventive. The other Michigan collections are from rock crevices in the Porcupine Mountains, Keweenaw Peninsula, Isle Royale, and Huron Mountains, where the species is more likely indigenous. But the status is not clear of such records as a single one from southwestern North Dakota (Stevens in Rhodora 74: 393.1972) or western Vermont (Weatherby in Rhodora 37: 411. 1935)—the latter in a thoroughly lumbered area and the collector not convinced that the species was native there.

Great Lakes distribution of
25. *Collinsia parviflora.*

26. *Goodyera oblongifolia* Raf.   Rattlesnake-plantain

This orchid is another far-ranging species in our area, like *Rubus parvi-florus,* growing in moist to dry coniferous and deciduous woods, rich or sandy soils, especially near the Great Lakes shores. Its habitat is similarly variable in the west, where it is found from Alaska south to California, New Mexico, and Mexico. It is isolated in the Black Hills, and found east of the Great Lakes from Gaspé and Lake St. John south to Nova Scotia, northern Maine, and Vermont. The map by Luer (1975, p. 142) does not show the disjunction between the Great Lakes and the west, which is clear in the small map by Hultén (1968, p. 328) and the detailed one by Kallunki (1976, p. 58).
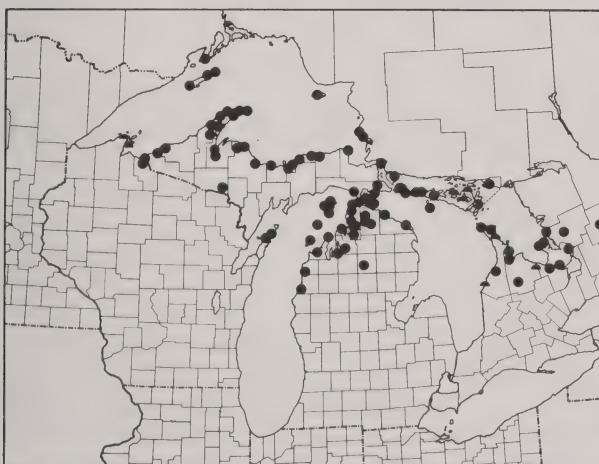
Great Lakes distribution of
26. *Goodyera oblongifolia.*

27. *Habenaria unalascensis* (Sprengel) S. Watson   Alaskan Orchid

   The Alaskan orchid, also known as *Piperia unalascensis* (Sprengel) Rydb., has a unique eastern distribution that begins at the eastern tip of the Upper Peninsula of Michigan and goes across Drummond Island, Manitoulin Island, and south to the Bruce Peninsula. Case (1964, p. 65) suggests that it is undergoing a population explosion, for old records are scarce, while it is now locally common in its choice habitat: dryish, rock-rubbled brushlands and open, thin forest. Apparently clearing, lumbering, and burning have favored this species. In the west it occurs from the Aleutians all the way south to Mexico (Baja California) and Colorado. It is disjunct in calcareous habitats in the Black Hills, and occurs again on Anticosti Island in the Gulf of St. Lawrence. The range of this species—as typical a cordilleran disjunct as any—is given in an early map by Fernald (1925, p. 255—omitting Black Hills and Michigan) and in later ones by Hultén (1968, p. 324) and Luer (1975, p. 164).


Great Lakes distribution of 27. *Habenaria unalascensis.*

28. *Osmorhiza chilensis* H. & A.   Sweet Cicely

   This is another of the classic cordilleran disjuncts, discussed by Fernald and others—often under the name *O. divaricata*. Basically a woodland plant, it has a relatively large range of habitat in our area, like *Goodyera oblongifolia*—rich, moist woods to dry open deciduous woods, sometimes over limestone, and occasionally dunes and sandy bluffs. It is common from the Bruce Peninsula through northern Michigan, less frequent on the Ontario side of Lake Superior, in Minnesota (Cook Co., J. C. Jones in 1870, MICH—see Voss 1978, p. 55, the station recently confirmed by Morley, pers. comm.), and in Wisconsin (Read, 1976). In the west, it occurs from the Aleutians and southern Alaska to southern California and Colorado, as well as in the Black Hills. Its eastern range is from Newfoundland to New Hampshire. And in South America it is in Argentina and Chile. Maps have been published by Fernald (1925, p. 255), Constance and

Shan (1948, p. 136), and Hultén (1968, p. 697). Specimens have frequently been found misidentified as *O. depauperata* (*O. obtusa*), discussed below. The latter has the fruit more or less convex toward the apex, which is not beaklike, and the young fruit is without a subapical constriction; in *O. chilensis,* the mature fruit is definitely concavely tapered to a short beaklike apex and even the young fruit has at least a slight subapical constriction.

Great Lakes distribution of 28. *Osmorhiza chilensis.*

Additional taxa which might be mentioned here as once thought to be disjunct or raising special problems include *Corallorhiza striata* Lindley, now known to be much more continuous than once thought across the continent, especially in Canada (see Scoggan 1978, p. 528). Similarly, *Osmorhiza depauperata* Phil. (long known as *O. obtusa*), once thought to be nearly as disjunct as *O. chilensis* (see maps by Constance & Shan 1948, p. 136; Hultén 1968, p. 698), is too widespread in northern Ontario (to James Bay) and westward to be considered with our other disjuncts. It is, incidentally, much less common in our area than *O. chilensis. Pteridium aquilinum* var. *pubescens* Underwood is a taxon of dubious status within a nearly ubiquitous species, intergrading with the common var. *latiusculum* (Desv.) Underw., but reported as disjunct from the west in the Black Hills, the Great Lakes (northern Michigan and the Bruce Peninsula), and Megantic County, Quebec (see Tryon in Rhodora 43: 24 [map], 29–30. 1941). *Woodsia oregana* D. C. Eaton may be somewhat disjunct, but stations in Iowa and more or less all across Minnesota give it a peculiar pattern. *W. scopulina* D. C. Eaton also has stations beyond the range categories of the disjuncts in question, being known from Arkansas and the Appalachians of North Carolina, Tennessee, Virginia, and West Virginia (see Brown in Beih. Nova Hedw. 16: 92. 1964).

DISCUSSION

While our primary aim has been to update knowledge of the distribution of these species in the Great Lakes region, we should review briefly some ideas and theories which have been proposed to explain the distribution patterns. All discussions on this subject must begin with the effects of the Wisconsinan glaciation which ended some 10,000 years ago in the northern Great Lakes area. The present flora of the region is the result of invasion of the land previously covered by glacial ice—and often, subsequently, glacial and postglacial lakes. There is no evidence at this point which allows one to suppose that in this region there were "nunataks," or places of high elevation surrounded by the glaciers, where plants survived during glaciation and whence they were able to repopulate the adjacent territory. Fernald (1925 & 1935) based his explanation for the perplexing distributions of cordilleran species far to the east on a belief in such refuges.

Fernald's nunatak hypothesis has been repeatedly rejected not only for lack of geological evidence but also on phytogeographical grounds, for with increased knowledge of distributions many of his critical species have been found to occur far from the alleged nunataks and even near the centers of glaciation. (Concise summaries, with references, are given by Deevey in Bull. Geol. Soc. Am. 60: 1379–1382. 1949; and Butters & Abbe 1953, pp. 69–72. See also Damman in Rhodora 67: 384. 1965; and Wood 1972.) Alternative possibilities to explain these distributions include two general hypotheses, neither of which is necessarily exclusive of the other, depending on the preglacial distribution of the species involved.

One explanation is that the preglacial distribution of these disjunct species was basically western, where the bulk of the range is today, and that they migrated eastward along the retreating ice front, in a zone which presented new colonization areas relatively free from competition. Their subsequent disruption in range and isolation of populations would have occurred partly as a result of competition with newly arriving species and partly as a result of the xerothermic or hypsithermal period which took place in early postglacial time and would have eliminated suitable eastern habitats except where cool moist microclimatic situations existed, such as around the northern Great Lakes and in the Black Hills. This is the position of Fassett regarding *Rubus parviflorus*, for he concluded (1941, p. 346) "that the occurrence of the plant about the Upper Great Lakes is due, not to the survival of a preglacial flora on nunataks, but to migration across Canada during a postglacial cool period and subsequent bisection of the range by the aridity of the Great Plains." Kallunki (1976, pp. 56 & 58) accepts the same history for *Goodyera oblongifolia*. Whitehead (1972, pp. 130–131), in an interesting variation on this idea, suggests that some cordilleran taxa may have expanded their range to the east during times of glacial expansion, after which many populations were eliminated through competition, with possibly a northward dispersal of some western taxa. Any theory which involves migration of plants from the west to the Great Lakes must deal with two facts: the absence of east-west animal migration patterns, meaning that seed-dispersal mechanisms dependent on animals would be less effective; and the presence of Lake Agassiz, which covered an area as large as

all the Great Lakes combined at its greatest, in parts of Manitoba, Ontario, Saskatchewan, Minnesota, and the Dakotas, and which would have to have been crossed or bypassed.[3] The taxa not found east of the Great Lakes are perhaps the more likely candidates to have had this migrational history. For plains species such as *Chamaerhodos nuttallii* this is an especially likely route. On the other hand, this pathway is more difficult to contemplate for woody species with fleshy fruits, such as *Oplopanax horridus, Vaccinium membranaceum,* and *Rubus parviflorus.*

The other major general explanation for the rise of the disjunct pattern is that previous to the last glacier the species were distributed more or less transcontinentally and during glaciation survived at the edges of the glacial front or in the "Driftless Area" of Wisconsin. They could then reinvade the newly uncovered terrain as the glacier retreated. The discontinuity in range resulted either because the plants could not reinvade certain areas—for any of a large number of possible reasons—or because they died out during subsequent unfavorable conditions, as in the previous theory. Those taxa which occur also far to the east of the Great Lakes might be more likely to have had this kind of history, especially those which seem to be relics of a boreal or arctic-alpine zone, such as *Dryas drummondii, Arenaria macrophylla,* and several of the species not included in our list because of far northern stations, but merely mentioned earlier. Miller and Thompson (1979, p. 190) found abundant leaves of *Dryas drummondii* (along with the more widespread *D. integrifolia* and other arcticalpine or boreal species, some of which show an east-west disjunction today) in a sediment deposit in Vermont, dated at about 11,500 years ago, when the continental ice margin was in the St. Lawrence valley. Such fossil evidence shows that some species with an east-west distribution pattern grew on recently deglaciated surfaces south of their present occurrence and may have had a long history in the east. Continued investigation of late-glacial and interstadial deposits containing macrofossils is revealing much about the Pleistocene history of many plant species, especially ones now found a greater or lesser distance to the north. And in many instances further investigation of microfossils will also prove important (Whitehead 1972). But in the absence of so clear a fossil record for the other species under present consideration, it is not as possible as it is for *D. drummondii* to assign them with any certainty to any particular migration route. Just as absence of full data on present distributions has misled botanists to conclusions, so is lack of evidence of *past* distribution a basic problem.

Crum (1966, p. 41), in considering the small but interesting group of northern and cordilleran disjunct bryophytes, especially calciphiles, around Lake Superior and the St. Lawrence, suggests that "they are relics of glacial retreat persisting where they do because the habitats are right and there is no ecological pressure to move on." Noting that, as with vascular plants, it "is difficult to separate northern disjuncts from Cordilleran types," he (1972, p. 294) also allows that some few of these bryophytes "may be western-montane rather than

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[3]Many relevant considerations are found in "Life, Land and Water. Proceedings of the 1966 Conference on Environmental Studies of the Glacial Lake Agassiz Region," ed. by William J. Mayer-Oakes (Occ. Pap. Dep. Anthrop. Univ. Manitoba 1. 1967. 416 pp.)

arctic in origin, having resulted from an east-west exchange of species along the melting edge of the glacier. These species are not all calciphiles and could have belonged to a Cordilleran flora predating the Pleistocene." There is no reason to suppose that the history of higher plants has been fundamentally different from that of cryptogams with similar distribution patterns. Schofield (1969, pp. 196–200) reviews concisely (though with erroneous attribution of quotation to Stebbins) some ideas relating to cordilleran disjuncts, both bryophytes and vascular plants, and concludes that the "most plausible explanation of their disjunction is that the eastern representatives are remnants of a more wide-spread flora of the past, possibly of pre-Pleistocene arctic-alpine distribution in North America."

The disjunct species discussed here are only a small, specialized group within a broader east-west pattern, recently reviewed by Wood (1972, pp. 114–116). Yet even these few species represent great taxonomic diversity, occur in a diversity of habitats, and possess adaptations suggesting diverse means of dispersal. In terms of seed-dispersal strategies, the bright red presumably bird-dispersed fruits of *Oplopanax,* the wind-carried spores of *Cryptogramma crispa,* and the grains of *Poa canbyi* certainly did not allow these three species to reach Isle Royale and nearby shores (but nowhere else in the region) by the same route and at the same rate once they were available for colonization following submergence in a postglacial lake! This is but one example of the difficulty in making correlations between present distribution, habitat, and dispersal means. (Stebbins 1935, p. 70, early noted dispersal issues for these plants in the Bruce Peninsula.) There *is* a floristic element of western affinity in our area, and some of the species demonstrate more or less striking disjunction from the west. But there is no evidence that these species arrived at the Great Lakes as part of one general community or even at the same time. Each would only be able to colonize newly deglaciated land at the time when specific conditions for it were favorable—and when it had been able to migrate (whatever its means and rate) from whatever place it survived glaciation. As our maps show, the resultant ranges about the Great Lakes today are quite diverse, some being extremely local and others much more widely distributed. We do not assume that most floristic elements defined by geographic criteria have necessarily arrived in our region en masse, whether western or Coastal Plain disjuncts, eastern deciduous forest species, littoral species, or Eurasian weeds! As to the taxa here considered, Dahl (1962) notes that some of the cordilleran species have specialized sub-strate requirements or are well adapted for long-distance dispersal—such as the tiny-seeded *Habenaria unalascensis* and *Goodyera oblongifolia* and the bristly fruited *Osmorhiza chilensis* of our list. As he suggests, the real core of cordilleran disjuncts, of persistent phytogeographic interest, will be species ill-adapted to long-distance dispersal and not transcontinental arctic or subarctic relics. Species of forested habitats, particularly the deciduous forest, rather than such pioneer situations as rock outcrops and lake shores, are the most challenging to explain as "boreal souvenirs."

SOURCES OF DATA AND ACKNOWLEDGMENTS

Solid circles on the maps represent specimens examined by one or both authors, primarily in the herbaria of The University of Michigan (MICH), Michigan State University (MSC), Cranbrook Institute of Science (BLH), Wayne State University (WUD), University of Michigan Biological Station (UMBS), and Isle Royale National Park (IRP), but with specimens of some species examined from additional herbaria in connection with the Michigan Flora Project and/or Michigan's Endangered and Threatened Species Program; in addition, some of the solid circles in Ontario represent records kindly confirmed or reported to us by A. A. Reznicek from brief examinations on our behalf at the National Herbarium of Canada (CAN), the herbarium of the University of Toronto (TRT), and the herbarium of the University of Guelph (OAC), as well as records from his own collections in Simcoe County. Half-circles on the maps represent additional important records from personal correspondence or literature records considered reliable. A number of old literature reports that could not be verified by specimens or recent correspondence are not repeated on the maps. Symbols on the maps do not necessarily represent the total number of known collections, since there may be several collections from the same site or from sites so close together that additional symbols would only result in excessive overlapping on the scale used.

The base map was supplied through the courtesy of the Cranbrook Institute of Science, and was first used in Case (1964).

Works relied upon rather heavily for details of distribution in the Great Lakes region, but outside of Michigan, and hence the source of many of the half-circles, include Butters and Abbe (1953), Krotkov (1940), Lakela (1965), Morton (1977), Read (1976), and Taylor (1938). For overall ranges in North America we have attempted to reconcile statements and maps in numerous local floras, such as Dorn (1977) and Van Bruggen (1976), along with more general works including Boivin (1967), Fernald (1925, 1935, & 1950), Gleason (1952), Hultén (1968), Hitchcock and Cronquist (1973), Richards (1952), and Scoggan (1978–1979).

For valuable information received via correspondence or discussion, we are grateful to A. A. Reznicek (University of Michigan), Robert H. Read (Wisconsin Department of Natural Resources), Thomas Morley (University of Minnesota), Rolla M. Tryon (Harvard University), John McNeill and W. G. Dore (Agriculture Canada), and James S. Pringle (Royal Botanical Gardens, Hamilton, Ontario). While we put specific questions to most of these individuals, only we are responsible for any omissions or other errors resulting from failure to ask other questions or to consult the right literature.

This paper was originally prepared by the first-named author as a senior honors thesis at The University of Michigan in 1975. It has been thoroughly revised and updated by collaboration of both authors in 1980.

APPENDIX

By way of an index and summary, and to call attention to the status of many of the disjuncts in these days of concern about threatened and endangered species, the following table lists in alphabetical order the 29 species discussed, with the consecutive number of the species, the geographic group to which it is assigned (I–A, I–B, II–A, II–B, as discussed in the introduction), and the status in Michigan, Wisconsin, and Ontario as designated in published reports.

Name	Group	Michigan[1]	Wisconsin[2]	Ontario[3]
8. Adenocaulon bicolor	I–B			R
1. Agropyron spicatum	I–A	EXT		
14. Arabis holboellii	II–A			R
15. Arenaria macrophylla	II–A	T	E*	R
9. Arnica cordifolia	I–B	E		R
24. Arnica lonchophylla	II–B			R
10. Ceanothus sanguineus	I–B	T		
2. Chamaerhodos nuttallii	I–A	E		
25. Collinsia parviflora	II–B	T		R
3. Crataegus douglasii	I–A	R		R
4. Cryptogramma crispa	I–A	T		R
5. Disporum hookeri	I–A	T		
16. Dryas drummondii	II–A			R
6. Festuca occidentalis	I–A		E	R
17. Galium kamtschaticum	II–A			R
26. Goodyera oblongifolia	II–B			R
27. Habenaria unalascensis	II–B	T		R
11. Melica smithii	I–B		E	R
18. Mimulus moschatus	II–A			R
7. Oplopanax horridus	I–A	T		R
28. Osmorhiza chilensis	II–B		T	R
19. Poa canbyi	II–A	T		R
20. Polygonum douglasii	II–A			
21. Polystichum lonchitis	II–A			R
22. Pterospora andromedea	II–A	T	E*	R
12. Rubus parviflorus	I–B			
13. Vaccinium membranaceum	I–B			
23. Vaccinium ovalifolium	II–A			R

[1]See Wagner et al. (1977). Species listed as endangered (E) came under full protection of Michigan's Endangered Species Act of 1974 on Dec. 2, 1976; those listed as threatened (T) were formally covered on Feb. 5, 1980; those listed as probably extinct in the state (EXT) or rare (R) have no formal protection under the law.

[2]See Read (1976) and "Endangered and Threatened Species List," Wis. Dep. Nat. Resources, 1980. An asterisk in this column indicates species receiving protection under Wisconsin's Endangered and Nongame Species Act as of Oct. 1, 1979; other designations are still advisory.

[3]See Argus & White (1977). The only category thus far indicated is "Rare" and the species have no legal protection, pending further evaluation.

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EFFECT OF GAMMA RADIATION ON USNIC ACID RETENTION IN CLADINA MITIS

George E. Funkey

Academic Computing Services

and

Frederic H. Erbisch

Dept. of Biological Sciences and Keweenaw Research Center
Michigan Technological University
Houghton, 49931

The effect of acute gamma radiation on the retention of the lichen substance usnic acid by *Cladina mitis* was determined. A ferric chloride colorimetric test was used to determine the concentration of usnic acid. No significant concentration changes were noted in podetia up to 4 months following irradiation to 1000 krad. Podetia irradiated to 1000 krad did have a significant decrease (70%) in usnic acid content after 9 months, but this decrease may be considered an indirect effect of irradiation. The data strongly suggest that gamma radiation, up to 1000 krad, has no immediate direct effect on usnic acid retention.

Previous gamma radiation studies with lichens have shown that little or no physical damage is seen until the lichen passes through a prolonged period suitable for growth (Barstow & Erbisch, 1977; Erbisch, 1978; Erbisch, 1977; Erbisch & Kalosis, 1973; Erbisch, Ligon & Mathena, 1977; Pullem & Erbisch, 1972). Physical damage of podetia includes loss of tensile strength, decrease in number of algal cells, changes in podetial pigmentation and flattening of podetia. While morphological damage is not manifested soon after radiation, physiological damage is, particularly the rate of photosynthesis (Barstow & Erbisch, 1977). In the continuing study of the effects of gamma radiation on lichens it was felt that another parameter to be examined was the immediate and long-term effects of radiation on lichen-substance retention in the intact organism. Many lichen substances are found in crystalline form outside of the mycobiont protoplast (Hale, 1969). Gamma radiation may directly or indirectly affect the retention of the lichen substance or have no effect. A direct effect would involve a change in the plasma membrane or the hyphal cell wall so that the substance could be lost soon after irradiation. Indirect effects would include a change in metabolism which in turn would, in some way, affect lichen substance retention. Changes in lichen substance content perhaps could serve as an indicator of radiation damage prior to the manifestation of physical damage.

Usnic acid, a common lichen substance found in *Cladina mitis* (Sandst.) Hale & Culb., provided the basis for such a concentration-retention study. Also, because of the previously determined physical and physiological affects of gamma radiation on *C. mitis,* any usnic acid concentration differences might be correlated with this damage to develop a more complete picture of the effects of gamma radiation on the lichen.

Cladina mitis podetia were taken from the Sedar Bay region of Keweenaw County, Michigan, in June and November. Thalli which were to be irradiated were divided into four samples each. One sample served as the control. The other three were irradiated when moist with 10, 100, or 1000 krad in a Gamma Cell 200 (^{60}Co, 500 rad/min). Some control and irradiated thalli were placed in a field, an open meadow, for several months near the University to determine the effect of time on usnic acid retention. The remaining thalli were examined within 48 hours after irradiation. A total of 15 podetial clumps were collected and irradiated; of these eight were used in the long-term experiment, and the remainder were used for determination of the immediate effects of irradiation.

Since a high pressure liquid chromatograph was not available, ferric chloride hexahydrate ($FeCl_3 \cdot 6H_2O$) was used as a colorimetric indicator for usnic acid (Laakso & Gustaffson, 1952). For this test 1 ml of 5% ferric chloride in acetone was added to 10 ml of an usnic acid-acetone solution, and immediately after mixing absorbance at 452 nm was read. The reliability and repeatability of this test were evaluated using a series of usnic acid (Nutritional Biochemicals Corp.)—acetone solutions ranging from 10^{-3}M to 10^{-5}M. The tests were repeated at least four times. Results of the ferric chloride test (Fig. 1) proved the method to be acceptable for use in testing the usnic acid content of large samples of podetia.

Prior to usnic acid analysis, irradiated and control podetial mats were dried at room temperature for 4 to 6 hours. Then they were dried 20 to 24 hours in a desiccator over sulfuric acid to a constant weight. One-gram samples of dried whole podetia, from base to tip, were used to obtain average usnic acid concentrations. A dried podetial sample was crushed, placed in a flask and shaken with 100 ml of acetone for 15 minutes. The resultant solution was filtered into a 200 ml volumetric flask. The filter was rinsed with fresh acetone; and this rinse and additional fresh acetone were added to fill the volumetric flask. Usnic acid content of this acetone solution was measured at 452 nm using the ferric chloride method. Since chlorophyll b (abs. max. 453 nm) is found in the green algal phycobiont of *C. mitis* (Rabinowitch & Grovindjee, 1969) 10 ml aliquots of the extract were read with 1 ml of acetone against an acetone blank to determine the amount of chlorophyll b absorbance. Separate 10-ml aliquots were then read with 1 ml of 5% ferric chloride reagent against a ferric chloride blank to determine the absorbance of usnic acid and chlorophyll b. The amount of usnic acid was then computed from these absorbance figures by subtracting the chlorophyll b absorbance from the total absorbance. Results are the means of at least 6 individual lichen samples from different clumps.

Three sets of lichens were analyzed: Lichens collected in November and examined immediately after irradiation; lichens collected and irradiated in November and harvested in March (4 months after irradiation); and lichens collected and irradiated in June and harvested in March (9 months after irradiation).

Figure 2 shows the mean percent usnic acid per gram dry weight for control and experimental samples. The means for samples tested immediately after irradiation were 1.0% for control, 1.49% for 10 krad samples, 1.81% for 100 krad samples and 1.56% for 1000 krad samples.

Figure 3 shows the results of the samples irradiated in June and November and then tested in March. The mean concentration of usnic acid for these groups was 1.38% for control, 1.58% for 10 krad samples, 1.38% for 100 krad samples, and 1.54% for 1000 krad samples. The podetia which had been irradiated in June to 1000 krad and analyzed in March had a mean usnic acid content of 0.38%.

The analysis of variance (Alder & Roessler, 1968) indicated that only the lichens irradiated in June and tested in March were significantly different in usnic acid concentration.
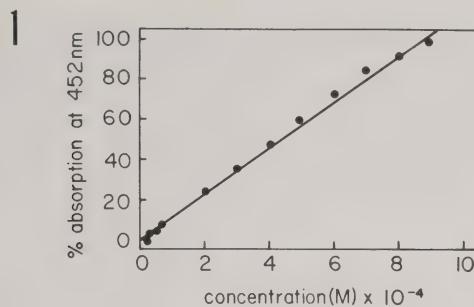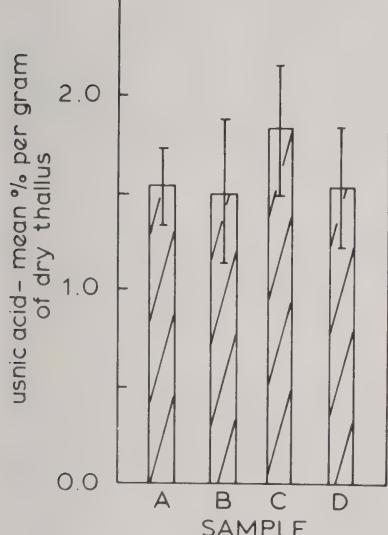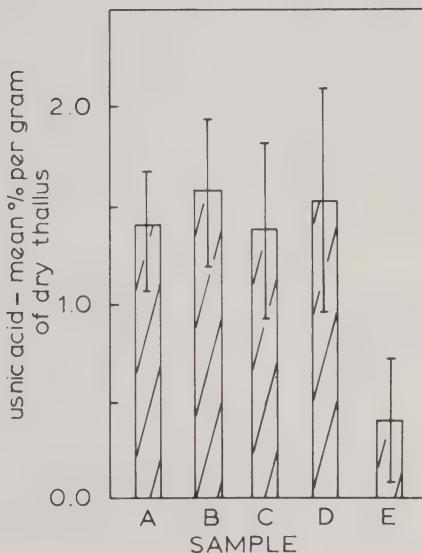
FIG. 1. Results of the % absorption of standard usnic acid solutions test using a ferric chloride colorimetric analytical technique. Each solid circle represents the mean of at least four analytical runs. Standard deviations ranged from 0.5 to 4.0% with the larger deviations being exhibited by the highest concentration of usnic acid. The line represents the least squares regression of known concentrations of usnic acid vs. absorbance of 452 nm. The equation of the line is: concentration = (0.00064 X absorbance) - 0.00002 (r^2 = 0.98). FIG. 2. Results of the *in vivo* analysis of usnic acid from *Cladina mitis* podetia, given as means % per gram of dry thallus. All samples were tested immediately after irradiation. The hairline indicates one standard deviation within each group; A = control group, B = podetia irradiated to 10 krad, C = podetia irradiated to 100 krad, D = podetia irradiated to 1000 krad. FIG. 3. Results of the *in vivo* analysis of usnic acid from *Cladina mitis* podetia, given as mean % per gram of dry thallus. Samples A–D were irradiated in November and Sample E was irradiated the previous June. All samples were tested the following March (4 and 9 months after irradiation). The hairline indicates one standard deviation within each group; A = control, B = podetia irradiated to 10 krad, C = podetia irradiated to 100 krad, D and E = irradiated to 1000 krad.

No physical damage related to the irradiation was seen in any of the lichens examined within 48 hours of radiation. June-irradiated podetia exhibited no damage prior to the time the November-irradiated ones were placed in the field. Because of the deep snow cover (> 100 cm), no damage was observed until the lichens were brought into the laboratory for usnic acid analysis. Damaged podetia were flattened and yellowish as compared with controls. The damage appeared more severe in the June-irradiated lichen.

The results indicate that gamma radiation had no immediate effect on usnic acid retention. The lichens placed back in the field for nine months after irradiation showed a decrease in usnic acid level, yet those placed back in the field for four months after irradiation did not. Because there were no concentration changes immediately or up to four months after irradiation, it is assumed that there was no direct radiation effect on usnic acid retention. The fact that usnic acid levels decreased after nine months suggests that physiological and/or physical changes directly attributable to gamma radiation may have affected retention. Also, the environmental conditions coupled with gamma radiation damage could perhaps account for the observed usnic acid concentration difference.

Transplanting podetia had no effect on retention. Podetia examined soon after collection and field controls examined four and nine months after transplanting did not have significant differences in usnic acid levels. Therefore, the loss of usnic acid observed nine months after irradiation was due, directly or indirectly, to the gamma radiation.

All of the November and June irradiated lichens when removed from the field in March also showed obvious morphological changes indicative of an unhealthy state. This deterioration could have been caused by an increased biochemical demand on the organisms during a period of growth. The greater growth demand on the June irradiated lichens then affected usnic acid levels. Since physical damage was noted prior to a change in usnic acid levels, i.e., in the November irradiated podetia, the usnic acid test is not of value in assessing immediate radiation damage in *Cladina mitis*. Although the podetia evidenced physical damage, they were not visibly rotted or decayed. The retention of usnic acid, a compound known for its antibacterial properties (Culberson, 1969; Vartia, 1973), may prevent the microbiological deterioration of the damaged podetia. The retention of usnic acid may serve as a means of protecting the slow-growing lichen from microbiological deterioration so that recovery of all or a portion of the damaged thallus could be possible.

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GNAPHALIUM SYLVATICUM (COMPOSITAE) NEW TO WISCONSIN

Robert W. Freckmann

Dept. of Biology
University of Wisconsin—Stevens Point
Stevens Point, 54481

William J. Fraundorf

College of Natural Resources
University of Wisconsin—Stevens Point
Stevens Point, 54481

On September 18, 1978, while completing a summer of field work on Outer Island, outermost of the Apostle Islands, in Lake Superior, the junior author collected an unknown *Gnaphalium* (cudweed or sweet everlasting) later identified by the senior author as *G. sylvaticum* L. The species, new for the Wisconsin flora, is readily distinguishable from most other *Gnaphalia* of the upper midwest because of slender, spikelike inflorescences (in contrast to flat-topped

or spreading inflorescences). *Gnaphalium purpureum,* which also has a slender inflorescence and has been reported from southern Illinois and southern Ontario (Scoggan, 1978), is an annual with broader basal leaves. The superficially similar *Filago arvensis,* fluffweed, is a fairly recent Eurasian introduction established in Michigan (Gleason & Cronquist, 1963) and the northwestern states (Hitchcock et al., 1955). It differs from *Gnaphalium sylvaticum* in having fewer heads (usually less than 10 vs. 30 or more) and few hairy involucral bracts with green midribs, about as long as and intergrading into receptacular bracts which partially enclose pistillate flowers, in contrast to numerous glabrous brown and scarious-margined involucral bracts of various lengths surrounding a naked receptacle.

The *Gnaphalium sylvaticum* population consists of a few individuals located in section 34, T53N, R1W, in the interior of the island about 100 m from a beaver impoundment. The population does not appear to be a recent introduction by man. It was found growing in partial shade on moist soil, among mosses and sedges, associated with *Habenaria clavellata, H. psycodes,* and *Spiranthes cernua.* The site lies between a logging trail which was probably last used in about 1960 and a young woods of *Acer rubrum* and *A. spicatum.* The entire island has received little impact from human activities or other disturbance, except for a few small fires and the creation of impoundments by beaver, in the past two decades and is uninhabited. The known vascular flora of the island consists of 272 taxa (Anderson et al., 1979) and includes the following species considered for threatened or rare status in Wisconsin (Read, 1976): *Arethusa bulbosa, Cypripedium calceolus, Deschampsia flexuosa, Osmorhiza chilensis, Parnassia palustris,* and *Rhynchospora fusca. Gnaphalium sylvaticum* can be added to that list.

The reported range (Fernald, 1950; Scoggan, 1978) of *Gnaphalium sylvaticum* includes western Asia, northern Europe, Iceland, northern New England, and eastern Canada west to the Nipissing and Muskoka districts of eastern Ontario. The Apostle Island population thus represents a range extension of approximately 800 km.

One specimen is deposited at University of Wisconsin—Stevens Point (UWSP) and a second at the University of Wisconsin—Madison (WIS).

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TWO LITTLE KNOWN NORTH AMERICAN STIPITATE HYDNUMS

K. A. Harrison

Herbarium, University of Michigan
Ann Arbor, 48109

and

Dept. of Biology, Acadia University
Wolfville, Nova Scotia

Hydnum ustale K. Harrison was described (1964) from collections made by Ingrid Bartelli on the sandy pine plains at the shore of Lake Superior near Marquette, Michigan. It was placed in synonymy with *Sarcodon (Hydnum) leucopus* (Pers.) Maas G. & Nannfeldt (1969) in their treatment of the genus *Sarcodon* in Sweden. Maas Geesteranus later (1975) expanded his concept of this species to include collections from Switzerland and Italy and published a description and two colored plates; his plate 27 illustrates a large specimen found in Switzerland and plate 28 three sporocarps from Norway.

Before *H. ustale* was described portions of two collections of *H. laevigatum* from Sweden identified by S. Lundell were examined and recognized as a taxon occurring in the Pacific Northwest. Duplicates of these Swedish collections are among the material reported as *Sarcodon leucopus* (Pers.) Maas G. & Nannf. I have accepted the name change to *Hydnum leucopus* Pers. for the American species but do not agree that *H. ustale* is conspecific. After I learned of the name change, another collection made by Lundell in Uppland, Danmark parish, near Svedden, 4 Sept. 1936, was obtained through the kindness of Dr. Nannfeldt. In this paper the two American taxa are redescribed and compared with authentic material of *Sarcodon leucopus* (Pers.) Maas G. & Nannf.

The spore measurements presented in this paper include the tubercles exclusive of any that resemble the apiculus. SEM photographs recently made by the author support the assumption that the tubercles are an integral part of the spore. It is theorized that they are expansions of weak (thinner) areas in the spore wall and develop as diverticula under the pressures created when the cytoplasm is forcibly extruded into the young spore by the basidium.

The name *Hydnum* Fr. is used instead of *Sarcodon* Quél. as it was introduced by Linnaeus, accepted by Fries in 1821, and confirmed by S. F. Gray in 1821.

Hydnum ustale K. Harrison, Canad. Jour. Bot. 42:1215. 1964.   Fig. 1

non *Sarcodon leucopus* (Pers.) Maas G. & Nannf. *in* Svensk. Bot. Tidskr. 63:415. 1969; misapplication as *Sarcodon laevigatus* (Swartz) Karst. by Coker & Beers, p. 49, Pl. 30. 1951.

Fig. 1. *Hydnum ustale* K. Harrison, near Marquette, Michigan, *Harrison 9917*, October 2, 1970 (larger cap 13 cm. across), ✕0.7.

Pileus 6–21 cm, convex, plane to depressed with a wavy margin, rarely slightly eccentric; surface soft, matted fibrillose, areas nearly glabrous, center rimose, areolately cracked or slightly scaly; margin incurved when young, sterile becoming wavy and thin, smooth matted tomentose, with dark bruises following hail. Color Natal Brown* to Bister on disc, lightens outward to Warm Sepia, Wood Brown, Vandyke Brown, Tilleul Buff, or pallid Avellaneous or mottling of shades on margins, light streaks show on pileus where pine needles adhere, margin darkens on handling. Cracks on disc are Avellaneous. All parts tend to darken as the pileus matures, and the margin may become Snuff Brown. Context up to 3 cm thick with a slightly olivaceous compact layer (1 mm) supporting the spines, Vinaceous-Buff close to cutis, in youngest nearly white, older Tilleul Buff or slightly darker, cut surfaces become Avellaneous on standing, maggot tunnels Wood Brown. Faint pleasant odor and slightly farinaceous taste in one collection, no odor or taste in eight others. One young specimen with a puckery or slightly bitter taste.

Spines 3–9(12) mm, 1 per mm but in one collection varying from 1 to 2 per mm, often decurrent with underdeveloped spines, subulate, tips sharp, Avellaneous, stained brownish with faint lilac tint when bruised, strained blackish when in contact with duff. Color varying with angle of light, slowly darkening with age to Wood Brown.

Stipe 3–5 ✕ 1–3 cm, short, sometimes peg-like, terete to rarely flattened, glabrous; apex expanded, strongly so in larger specimens, rarely scabrous from underdeveloped spines, base usually blunt, whitish to Tilleul Buff, lighter colored than spines, staining brownish, quickly becoming Warm Sepia, matted fibrillose under lens, white mycelium in duff around base. Context Fawn or near Wood Brown, darker than in pileus, possibly browner because of maggot tunnels.

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*Ridgeway colors are capitalized.

Chemical reactions. KOH blackens surface and margin, sections darken then fade to olive drab. $FeSO_4$ slowly olive grayish on pileus and cutis of a section, but tramal tissues may or may not change. NH_4OH blackens surface but more slowly than KOH. Melzer's merely adds its own color. Reagents soak in quickly except for $FeSO_4$. Dried tissues revive better in Melzer's than in KOH.

Spores and Hymenium. Spores $6.5-8 \times 5.5-7 \mu$m, Wood Brown, Buffy Brown in heavy deposit, subglobose to oblong to slightly flattened, with heavy apiculus, compound-tuberculate; some irregularly cruciate, tubercles up to 1.5μm in height may be rounded or with multiple processes. Basidia $7-8 \times 25-30 \mu$m, 4-spored, sterigmata up to 5μm long.

Tramal characters. In the youngest collections the surface cells were dull olive brown, often with incrusted walls. End cells varied in size and shape, $5-5.7 \times 40-82 \mu$m, tips tapered or blunt, thickened or thin, occasionally with strongly amyloid granular contents. A few spots with inter- and intra-cellular debris turning very dark to black in Melzer's. The color of the cuticular hyphae varied in older collections and was often a dull rufus shade. The amyloid cells were overlooked when the species was originally described, but collections from Michigan were checked and the presence of amyloid cells was confirmed in the type (*Smith 66385*). Tramal hyphae loosely interwoven, inflated, $9-17 \mu$m in diameter with large clamps; hyphae in spines thin-walled, compact, parallel, with clamps few to scattered.

Gregarious, or rarely single, under *Pinus banksiana* on sandy, acid, podsolized soil, shore of Lake Superior, Marquette Co., Michigan.

Michigan: Ammirati (Harrison 9796), Bartelli 2072; Harrison 9875, 9917, 9970, 10075, 10108, 10142, 10191, 10232; Smith 66385 (type), 72783.

In 1970, this species was common in the original locality, a sandy *Pinus banksiana* forest east of Marquette, Michigan, and ten additional collections from the locality were secured for the University of Michigan Herbarium. The first specimens were found on 19 September, and the species was abundant during the month of October. It was found in partial "fairy rings," the largest arc containing 80 sporocarps in clusters of two to four in a sector some 35 feet long. Stipes usually were so short that the pileus was barely above the duff or spread out on it. In appearance and habit of growth, *H. ustale* closely resembled *Boletopsis grisea* (Pk.) Bond. & Sing. and *Hydnum scabrosum* Fr. The three species were locally abundant under the pines in this area at the same time.

The lake shore where *H. ustale* was found was an area of stabilized sand dunes supporting a rapidly growing young forest of *P. banksiana.* Undercover consisted of impoverished mats of grass, stunted shrubs, and extensive patches of *Cladonia.* The soil was almost pure sand, acid and low in calcium and plant nutrients, with a gray podsolized layer immediately beneath the duff. The sand where vegetation had been removed blew easily.

Hydnum leucopus Pers., Mycol. Eur. 2:158. 1825.   Fig. 2—3

In part: *Sarcodon leucopus* (Pers.) Maas G. & Nannf., Sv. Bot. Tidskr. 63:415. 1969. In part: *Hydnum laevigatum* Sw. *ex* Fr. *sensu* Fr., Monog. Hym. Suec. 2:275. 1863, *non H. laevigatum* (Sw. *ex* Fr.) Fr., Sv. Åtl. och Gift. Svampar. Pl. 81. 1860—66. *Hydnum laevigatum* Swartz, J. Bresadola Icon. Myc. 21: Pl. 1042. 1932. Non *Hydnum ustale* K. Harrison, Can. J. Bot. 42:1215. Pl. 2, fig. 4. 1964.
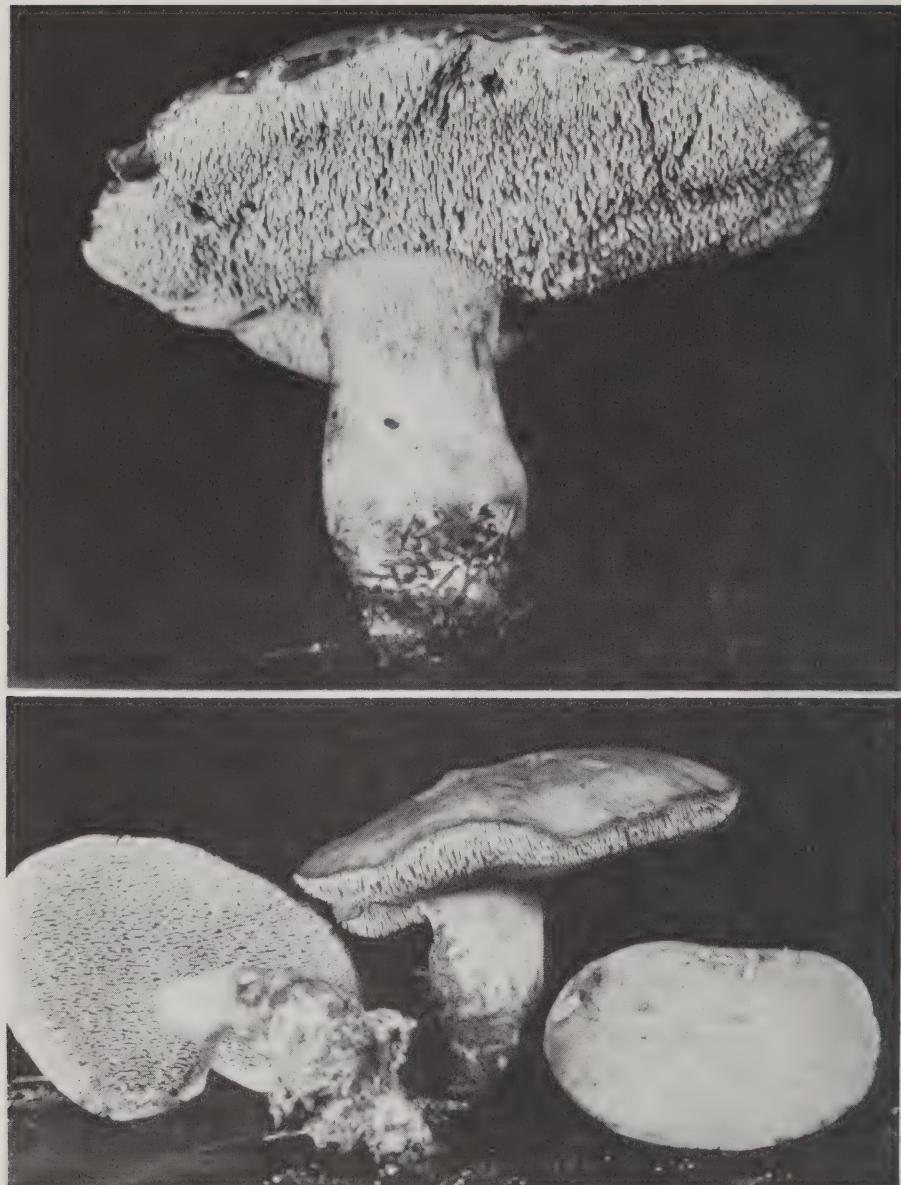
Figs. 2–3. *Hydnum leucopus* Pers., Whidbey Island, Washington, *Harrison 6455,* October 20, 1966. 2(above), 14 cm across cap, ×0.7. 3(below), 9 cm across cap. ×0.6.

Pileus 8–15(22) cm broad, convex to rarely plane, lobed to eccentric; surface dry, soft, subtomentose, cracking into small scales, in age in dry weather often with large dark, patch-like scales; Fawn Color, Light Cinnamon-Drab, Vinaceous-Drab, Wood Brown on disc in age; margin Pale Vinaceous-Fawn to Tilleul Buff, slowly blackening when bruised, incurved when young, sterile, faintly tomentose; context soft, not brittle, white to Tilleul Buff, in *Smith 58841* Dull Lavender, unchanging for some time but darkening to Pale Vinaceous-Fawn overnight. Odor slightly fragrant in some, none or faintly of urea in others, taste slightly bitter, strongly so in all dried specimens.

Spines up to 1.2 cm X 1 mm (1.7 cm long in Alaskan collection), free or slightly decurrent, close, Avellaneous becoming Wood Brown, Alaskan collections when bruised purplish after several hours.

Stipe 5–8 X 1–5 cm, eccentric, clavate when young, becoming equal, apex light Fawn Color with narrow band of scabrous dots from tiny spines, Avellaneous and whitish downward, unpolished, appressed-floccose, may stain brownish or lavender when bruised, base white mycelioid, context similar to that of pileus but often blackish in basal tip.

Chemical reactions. KOH negative or olivaceous on cutis and context, FeSO₄ slowly drab on cutis, negative on context.

Spores and Hymenium. Spores Wood Brown in mass. Size varying with area: Alaska, 6–7 X 5.5–6 µm; Washington, Hall & Stuntz, 6.4–7.5 X 5.3–6.4(7.4) µm; Idaho, 6.4–7.4(8.4) X 5–6.4 µm; California, 7–8 X 6–7 µm; New Mexico 7.4–8.5 X 6.3–7.4 µm; Sweden, Maas Geesteranus & Nannfeldt, (6.7)7.2–7.6 X (4)4.7–5.6 µm. The spores in Swedish collections, reported as flattened by Maas Geesteranus, are narrower than in American collections. Spores from a portion of the Swedish collection made by E. Th. Fries in 1950, MICH, 6–7 X 5–6(6.5) µm. Basidia 6.5–9 X 30–40 µm, clavate, tapering to a clamped basal septum, sterigmata up to 5 µm long. Hyphae in the spines 3.5–8(9) µm, closely parallel with clamps and many septa oblique.

Tramal characters. The cutis hyphae 3–5 µm wide, color oozes out when revived in KOH, hyphae in epicutis 7–10 µm wide, and in trama up to 16 µm but may be as narrow as 5 µm, numerous clamps, cell walls hyaline and thin. In Melzer's cutis and epicutis bright yellow.

Solitary or widely gregarious, under pines in California, New Mexico, and Idaho, mixed conifers in Washington and British Columbia, and spruce in Alaska.

Alaska: Wells 8–10–61 no.1; California: H. Lanphere 1960, Thiers 11068; Colorado: Smith 87060, 85968; Idaho: Smith 58841; 65666, 76643; New Mexico: Barrows 3070, Isaacs 2719, Harrison 6912, 6980, 7082; Washington: Harrison 6455, 6475, 6588, Smith 17871, 49187; British Columbia: Harrison 6174; Sweden: Uppland, near Svedden, S. Lundell, 4 Sept. 1936; Trakumla parish, Davidshage, E. Th. Fries, 29 Sept. 1949 & 23 Aug. 1950. Hall & Stuntz (1972) reported eight collections of *H. laevigatum* from the Puget Sound area.

Following is a comparison of characters that differ between the Western taxon accepted as *Hydnum leucopus* and *H. ustale* obtained from the type locality in Michigan:

H. leucopus	*H. ustale*
Pileus	
Often lobed or eccentric. Fawn Color to Vinaceous Drab. Margin Pale Vinaceous Fawn, blackening if bruised	Rarely eccentric. Natal Brown to Bistre. Margin Tilleul Buff, brownish if bruised
Context	
Slowly stains Pale Vinaceous Fawn. Odor unpleasant, taste slightly bitter, strongly so when dried	Staining Avellaneous on standing. Taste and odor mild

Stipe

5–8 X 1–5 cm, Avellaneous with blackish tip, slowly staining lavender to brownish

3–5 X 1–3 cm, Tilleul Buff quickly staining Warm Sepia

Spores

6.4–7.4(8.4) X 5–6.4 µm (Idaho)
6–7 X 5–6(6.5) µm (Sweden)

6.5–8 X 5.5–7.0 µm

The spore sizes given by Maas Geesteranus & Nannfeldt (1969) for *Sarcodon leucopus,* (6.7)7.2–7.6 X (4.5)4.7–5.4 µm, are distinctly narrower than those given here because, as I understand it, Maas Geesteranus carefully avoided including tubercles in his measurements. My measurements of *Hydnum* spores have always included the tubercles, avoiding only the apiculus. The information on *H. ustale* comes from ten collections selected from at least 1000 sporocarps growing in the Marquette area in 1970. (Specimens were seen on other pine plains on the shores of Lake Superior but were never as abundant as near Marquette.)

The Lundell collection of 1936 obtained from Dr. Nannfeldt was compared with *H. ustale:* The following microscopic details were found:

In *H. leucopus* the hyphae attached to the base of the stipe are repeatedly branched, thin-walled, variable in width with the narrower strands frequently collapsed. The clamps at the numerous septa are variable, ranging through slight overlapping to large, distinct clamps joining cells slightly inflated at the septa.

In *H. ustale* similar hyphae are thick walled, uniformly tubular, with septa widely spaced, with small hemispherical clamps. The cells are usually uniformly sized throughout and not collapsed. One patch of mycelium on the base of *H. leucopus* was blue-green in KOH, and some hyphae were "apparent amyloid" in Melzer's. Such hyphae were not found in the basal mycelium of *H. ustale.*

The stipes of both species are usually light-colored after drying. The surface of *H. leucopus* has numerous dark, scabrous dots extending from the rudimentary decurrent spines at the apex almost to the base of the stipe. The dots are clumps of dark basidioles or possibly caulocystidia projecting for some distance above the surface. They do not show any of the narrow, actively growing hyphae found in the tips of normal spines. Occasionally some cells were seen with sterigmata, but these were also seen on caulobasidia on the surface between clumps. *H. ustale* also had widely spaced abortive spines at the apex, but only for a short distance. The surface of the stipe was folded, and the clumps of caulocystidia were much smaller than in *H. leucopus.* In no case were sterigmata seen. The texture of the surface layer of the stipe of *H. leucopus* appeared granular (under the dissecting microscope); in *H. ustale* it was fibrous.

The outstanding field characteristics of *H. ustale* are the short stipe expanding into the pileus, the very light color of stipe and spines that stain brown promptly on handling. The light color of the stipe and spines is also a prominent feature in herbarium specimens, regardless of stage of maturity.

There are a number of differences in the description of *S. (Hydnum) leucopus* as published in 1969 and the broader description published in 1975. The colors as given in the latter could cover brownish colors of *H. ustale*. However, it is still maintained that *H. ustale* is a distinct, sharply-marked species as it grows in Michigan, where its natural appearance is that of a non-scaly *H. imbricatum* and after drying bears little resemblance to specimens from Sweden labeled *H. laevigatum* by Lundell. However, on being informed that Pl. 81, Fries 1866, of *H. laevigatum* was considered by Lundell to be a poor representation and that a second unpublished plate is closer to Lundell's idea of *H. laevigatum,* one might conjecture that Plate 81 may be an illustration of a species similar to *H. ustale.*

In summary, in North America *H. leucopus* is a rather tall, grayish-brown species tinged with vinaceous purple, and the flesh may become violaceous, while *H. ustale* is a squat, dark brown species and bruises brownish. The flesh is similar in both species in color and odor, but *H. leucopus* has bitter flesh especially after drying, while that of *H. ustale* is mild. There are microscopic differences in the tissues of the pileus. In Melzer's the cuticular hyphae of *H. leucopus* is golden-yellow, while in *H. ustale* the color is closer to rufus. In *H. ustale* there are dark inclusions that resemble (or are) amyloid material in some cuticular areas and in some hyphae. Such hyphae have not been seen in *H. leucopus.* However, mycelioid hyphae on the base of the stipe of one Swedish collection of *H. leucopus* gave a bluish KOH reaction and "apparent amyloid" hyphae were present. These reactions were not present in similar hyphae in *H. ustale.* There is also a probable difference in habitat, as *H. leucopus* in Europe is reported as possibly a calciphile, while *H. ustale* in America has been found only on highly acid soils and associated exclusively with *Pinus* spp.

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The January issue (Vol. 20, no. 1) was mailed February 20, 1981

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*On the cover: Udell Useen
of Ann Arbor reads braille plaque
in Nature Trail for the Blind
at Kalamazoo; photo by Clayton Alway*

COR/STA

THE

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THE FOURTH ANNUAL
A. H. SMITH LAKES STATES FORAY

J. F. Ammirati

Dept. of Botany
University of Washington
Seattle, 98195

Ingrid Bartelli   Nancy Weber

2010 Sugarloaf Ave.   University of Michigan Herbarium
Marquette, Mich. 49855   Ann Arbor, 48109

To date there have been five A. H. Smith Lakes States Forays, all in September or October. The first, held in Wisconsin's Kettle Morain State Forest, was organized by Harold Burdsall (Leslie, 1976). The second was held in Dixon Springs State Park in southern Illinois (hosted by Walter Sundberg), and the third at Lake Itasca, Minnesota (hosted by Elwin Stewart). The fifth, in the area of La Crosse, Wisconsin, in September 1979, was hosted by Allen Nelson. The fourth Foray took place at the Ford Forestry Center at Alberta, Baraga Co., in the Upper Peninsula of Michigan, on September 14–17, 1978. The Center, located nine miles south of L'Anse on Highway 41, is one of three departments of the School of Forestry and Wood Products of Michigan Technological University. Eric A. Bourdo, Jr., Dean of the School of Forestry, and Roger L. Rogge, Manager of Operations, Ford Forestry Center, did a fine job of preparing facilities for the foray. Housing and laboratory facilities were more than adequate, and the food, one of the main ingredients of a successful foray, was especially good. Bourdo gave an excellent talk on the history and activities of the Ford Forestry Center during the first evening.

The Center is ideally located for collecting fungi. Two miles west of the Center lies an extensive sand plain dominated by jack pine. Hardwood-hemlock stands dominate the area east of the Center, while stands of mixed hardwoods, aspen, and white birch, and both red and white pine are found immediately to the west. To the east and northeast sugar maples occur on the uplands, and white spruce-balsam fir-paper birch stands occupy poorly drained sites. Black spruce bogs occupy wet lowlands. A mile south are glacial till plains, largely cleared for agriculture; second-growth hardwoods and conifers grow where farms have been abandoned.

Heavy rains just before the foray produced a large crop of fleshy fungi on the sandy pine plains and generally good fruiting in other habitats. Gilled mushrooms dominated the flora in the pine plains, although boletes, hydnums, puffballs, and certain ascomycetes were also relatively abundant. Among the most common agarics on the pine plains were *Cortinarius mucosus, C. semisanguineus, Lactarius rufus, L. vinaceo-rufescens, Rozites caperata,* and *Tricholoma flavovirens. Lactarius paradoxus,* a species more frequent in the southeastern United States, was collected at several sites. A large fruiting of *Tricholoma (Armillaria) ponderosum* was found. It has been collected by the

FIG. 1. Participants of the 1978 foray. Photographed by Jim Weber. Left to right: *Standing:* Ingrid Bartelli, Joe Ammirati, Donna-Leigh Rendall, Don Rogers, Meredith Blackwell, Billie Rogers, Diana Parker, Alan Parker, Hal Burdsall, Adam Burdsall (child), Alex Smith, Henrietta Burdsall, Jena Burdsall (child), Helen Smith, Vivian Cooke, William Bridge Cooke, Clark Ovrebo, Robert Brown, Carole Wells, David Wells, Robert Fogel. *Kneeling:* Pam Johnson, Lisa Blackwell, Wanda Gillon, Nancy Weber, Barbara Christ, Mary Palm, Nina Johnson. *Missing from portrait:* Karen Nakasone, John Rippon, Tom Sullivan, Jim Weber.

senior author in sandy pine areas near Marquette, Michigan, and in central Québec, and it appears to be common in the Pacific Northwest. *Tricholoma cheilolaminum,* described from the West by Ovrebo & Tylutki (1975), is reported here for the first time from the Great Lakes region. Two hydnums, *Hydnellum caeruleum* and *Phellodon niger* var. *alboniger,* were locally common, and *Cordyceps ophioglossoides* (on *Elaphomyces granulatus*) was particularly abundant in one area of the pine plains, where dozens of fruiting bodies were found. *Laccaria trullisata* and *Scleroderma macrorhizon* were characteristic of loose sand slopes along roads through the pine plains. A large number of *Suillus* species were found, some on the pine plains, but others, such as *S. intermedius, S. pictus, S. placidus* and *S. punctipes,* in mixed woods containing white and red pine. *Cortinarius malicorius, C. armillatus, C. pholideus* and *C. collinitus* were also found in mixed woods, the last species in association with aspen. A large variety of *Hygrophorus* species were recorded; some, such as *H. puniceus,* grew in abundance in mixed woods. The woods were scoured for

polypores and others of the Aphyllophorales. Identifications were readily provided by William Bridge Cooke and Harold Burdsall.

Although several mycologists have collected extensively in the western Upper Peninsula, relatively few species lists have been published. Earlier reports of fungi from the western Upper Peninsula are given in Kauffman (1929) and Kauffman & Smith (1932). Both papers report fungi collected near Rock River, which lies east of Marquette on the south shore of Lake Superior. Many of the species on the foray list are documented by specimens in the Museum at the Ford Forestry Center (MCT-F), but the best collection of Upper Peninsula fungi is housed at the University of Michigan Herbarium (MICH).

A total of 32 people attended the foray (Figure 1). We were especially happy to have A. H. Smith, Helen V. Smith, William Bridge Cooke, and Donald Rogers in attendance. On the last day we were honored to have Mr. John Volker (*nom de plume:* Robert Traver), noted author and historian of the Upper Peninsula, join our group.

MYXOMYCOTINA
  Reticulariaceae
    Reticularia splendens Morg.
ZYGOMYCOTINA
  Mucoraceae
    Syzgites megalocarpus Fr.
ASCOMYCOTINA
  Clavicipitaceae
    Cordyceps ophioglossoides (Fr.) Link
  Diatrypaceae
    Diatrype stigma Fr.
  Elaphomycetaceae
    Elaphomyces granulatus Fr.
  Geoglossaceae
    Neolecta irregularis (Pk.) Korf & Rogers
  Helvellaceae
    Helvella crispa Fr.
    H. macropus (Fr.) Karst.
  Hyaloscyphaceae
    Lachnellula suecica (Fckl.) Nannf.
  Hypomycetaceae
    Hypomyces aurantius (Fr.) Tul.
    H. lactifluorum (Fr.) Tul.
  Leotiaceae
    Ascotremella faginea (Pk.) Seav.
    Bisporella citrina (Fr.) Korf & Carp.
    Chlorociboria aeruginosa (Fr.) Ram., Korf & Bat.
    Leotia lubrica Fr.
    L. stipitata Schroet.
  Pyronemataceae
    Aleuria aurantia (Fr.) Fckl.
    Neottiella rutilans (Fr.) Denn.
  Venturiaceae
    Apiosporina morbosa (Fr.) v. Arx
  Xylariaceae
    Daldinia concentrica (Grev.) Ces. & DN
    Xylaria polymorpha (Fr.) Grev.

BASIDIOMYCOTINA
  Hymenomycetes
  Agaricales
  Amanitaceae
    Amanita bisporigera Atk.
    A. citrina S.F. Gray
    A. flavoconia Atk.
    A. fulva Secr.
    A. muscaria (Fr.) Hook.
      var. alba Pk.
    A. porphyria (Fr.) Secr.
    A. rubescens (Fr.) S.F. Gray
    A. umbrio-lutea Secr.
    A. verna (Fr.) Vitt.
  Boletaceae
    Boletellus chrysenteroides (Snell) Sing.
    B. pallidus Frost
    B. piperatus Fr.
    B. pseudopeckii Smith & Thiers
    B. separans Pk.
    B. subglabripes Pk.
    B. subtomentosus Fr.
    B. subvelutipes Pk.
    Leccinum aurantiacum (St.-Amans) S.F. Gray
    L. scabrum (Fr.) S.F. Gray
    L. snellii Smith, Thiers & Watl.
    Suillus albidipes (Pk.) Sing.
    S. brevipes Kuntze
    S. granulatus (Fr.) Kuntze
    S. intermedius (Smith & Thiers) Smith & Thiers
    S. pictus (Pk.) Smith & Thiers
    S. placidus (Bon.) Sing.
    S. punctipes (Pk.) Sing.
    S. subluteus (Pk.) Snell
    S. tomentosus (Kauff.) Sing., Snell & Dick

Tylopilus chromapes (Frost) Smith & Thiers
T. felleus (Fr.) Karst
Coprinaceae
Coprinus comatus (Fr.) S.F. Gray
Psathyrella candolliana (Fr.) Maire
P. connisans (Pk.) Smith
P. subatrata (Batsch) Kühn. & Romag.
Cortinariaceae
Cortinarius alboviolaceus (Fr.) Fr.
C. anomalus (Fr.) Fr.
C. armillatus (Fr.) Fr.
C. bolaris (Fr.) Fr.
C. callisteus (Fr.) Fr.
C. callochrous (Fr.) S.F. Gray
C. collinitus (Fr.) S. F. Gray
C. distans Pk.
C. everneus (Fr.) Fr.
C. malicorius Fr.
C. mucigineus Pk.
C. mucosus (Fr.) Kickx
C. pholideus (Fr.) Fr.
C. semisanguineus (Fr.) Gill.
C. traganus (Fr.) Fr.
C. vibratilis (Fr.) Fr.
Gymnopilus penetrans (Fr.) Murr.
Inocybe fastigiata (Fr.) Quél.
I. lilacina (Pk.) Kauff.
Phaeocollybia lugubris (Fr.) Heim
Rozites caperata (Fr.) Karst.
Entolomataceae
Clitopilus prunulus (Fr.) Kumm.
Entoloma abortivum (Berk. & Curt.) Donk
E. sinuatum (Fr.) Kumm.
Gomphidiaceae
Chroogomphus superiorensis (Kauff. & Smith) Sing.
Hygrophoraceae
Hygrophorus borealis Pk.
H. conicus (Fr.) Fr.
H. flavescens (Kauff.) Smith & Hesl.
H. hypothejus (Fr.) Fr.
H. laetus (Fr.) Fr.
H. marginatus Pk.
var. olivaceus Smith & Hesl.
H. miniatus (Fr.) Fr.
H. nitidus Berk. & Curt.
H. niveus Fr.
H. parvulus Pk.
H. pratensis (Fr.) Fr.
H. puniceus (Fr.) Fr.
H. raei Maire
H. rainierensis Hesl. & Smith
H. russula (Fr.) Quél.
Lepiotaceae
Lepiota americana Pk.

L. clypeolaria (Fr.) Kumm.
L. cristata (Fr.) Kumm.
L. naucina (Fr.) Kumm.
Paxillaceae
Paxillus involutus (Fr.) Fr.
P. panuoides Fr.
Pluteaceae
Pluteus cervinus (Fr.) Kumm.
Russulaceae
Lactarius affinis Pk.
L. aquifluus Pk.
L. camphoratus (Fr.) Fr.
L. chrysorheus Fr.
L. deceptivus Pk.
L. deliciosus var. deterrimus (Grög.) Hesl. & Smith
L. lignyotus Fr.
L. mucidus Burl.
L. paradoxus Beards. & Burl.
L. proximellus Beards. & Burl.
L. pseudodeceptivus Hesl. & Smith
L. pubescens Fr.
L. resimus (Fr.) Fr.
L. rufus (Fr.) Fr.
L. subvellereus var. subdistans Hesl. & Smith
L. thejogalus (Fr.) S.F. Gray
L. thyinos Smith
L. torminosus (Fr.) S.F. Gray
L. uvidus (Fr.) Fr.
L. vietus (Fr.) Fr.
L. vinaceopallidus Hesl. & Smith
L. vinaceorufescens Smith
Russula brevipes Pk.
R. borealis Kauff.
R. brunneola Burl.
R. emetica (Fr.) S.F. Gray
R. lutea (Fr.) S.F. Gray
R. variata Pk.
R. xerompelina (Secr.) Fr.
Strophariaceae
Naematoloma sublateritium (Fr.) Quél.
Pholiota destruens (Brond.) Gill.
P. lubrica (Fr.) Sing.
P. spumosa (Fr.) Sing.
P. squarrosa (Fr.) Kumm.
P. squarrosa-adiposa J. Lange
Tricholomataceae
Armillariella mellea (Fr.) Karst.
Cantharellula umbonata (Fr.) Sing.
Clitocybe adirondackensis (Pk.) Sacc.
C. cerussata (Fr.) Kumm.
C. clavipes (Fr.) Kumm.
C. olida (Quél.) Konr.
C. robusta Pk.
Collybia butyracea (Fr.) Kumm.
C. confluens (Fr.) Kumm.

C. dryophila (Fr.) Kumm.
C. tuberosa (Fr.) Kumm.
Cystoderma amianthinum (Fr.) Fayod
Laccaria trullisata (Ellis) Pk.
Lentinellus ursinus (Fr.) Kühn.
Leucopaxillus albissimus (Pk.) Sing.
Lyophyllum decastes (Fr.) Sing.
L. loricatum (Fr.) Kühn.
Marasmius coherans (Fr.) Cke. & Quél.
M. fuscopurpureus (Fr.) Fr.
M. oreades (Fr.) Fr.
M. rotula (Fr.) Fr.
Mycena leaiana (Berk.) Sacc.
M. strobilinoides Pk.
M. vulgaris (Fr.) Kumm.
Oudemansiella radicata (Fr.) Sing.
Panus strigosus Berk. & Curt.
Panellus serotinus (Fr.) Kühn.
P. stipticus (Fr.) Karst.
Phyllotopsis nidulans (Fr.) Sing.
Pleurotus ostreatus (Fr.) Kumm.
P. ulmarius (Fr.) Kumm.
Tricholoma cheilolaminum Ovr. & Tyl.
T. flavovirens (Fr.) Lund.
T. imbricatum (Fr.) Kumm.
T. ponderosum (Peck) Sing.
T. portentosum (Fr.) Quél.
T. saponaceum (Fr.) Staude
T. sejunctum Quél.
Xeromphalina campanella (Fr.) Kühn. & Maire
Aphyllophorales
Cantharellaceae
Cantharellus cibarius Fr.
C. ignicolor Peters.
C. infundibuliformis Fr.
C. minor Pk.
Craterellus fallax Smith
Gomphus floccosus (Schw.) Sing.
Clavariaceae
Clavaria fusiforme Sower.
Clavariadelphus pistillaris (Fr.) Donk
C. sachalinensis (Imai) Corn.
C. truncatus (Quél.) Donk
Clavulina cinerea (Fr.) Schroet.
C. cristata (Fr.) Schroet.
Physalacria inflata (Fr.) Pk.
Ramariopsis kunzei (Fr.) Donk
Coniophoraceae
Coniophora arida (Fr.) Karst
C. puteana (Fr.) Karst
Coniophorella olivacea (Fr.) Karst
Corticiaceae
Amphinema byssoides (Fr.) J. Erikss.
Hyphoderma pilosum (Burt) Gilb. & Budd.
Hyphodontia alutaria (Burt) J. Erikss.

H. arguta (Fr.) J. Erikss.
H. aspera (Fr.) J. Erikss.
H. spathulata (Fr.) Parm.
Hypochnicium bombycinum (Fr.) J. Erikss.
H. punctulatum (Cke.) J. Erikss.
Laeticorticium roseum (Fr.) Donk
Leucogyrophana pinastri (Fr.) Ginns & Weres.
Peniophora polygonia (Fr.) Bourd. & Galz.
P. rufa (Fr.) Boidin
Phaneochaete sanguinea (Fr.) Pouz.
Resinicium furfuraceum (Bres.) Parm.
Trechispora farinacea (Fr.) Lib.
T. pallido-aurantica Gilb. & Budd.
Ganodermataceae
Ganoderma applanatum (S.F. Gray) Pat.
G. tsugae Murr.
Hericiaceae
Gloeocystidiellum porosum (Berk. & Curt.) Donk
Hericium coralloides (Fr.) S.F. Gray
H. ramosum (Mérat) Letell.
Auriscalpiaceae
Auriscalpium vulgare S.F. Gray
Hydnaceae
Dentinum repandum S.F. Gray
Hydnellum caeruleum (Pers.) Karst.
H. pineticola Harr.
H. scrobiculatum var. zonatum (Fr.) Harr.
Hydnum scabrosum Fr.
Phellodon niger var. alboniger (Pk.) Harr.
Hymenochaetaceae
Hymenochaeta tabacina (Fr.) Lev.
Meruliaceae
Merulius tremellosus Fr.
Phlebia radiata Fr.
Plicaturopsis crispa (Fr.) Reid
Mucronoporaceae
Inonotus tomentosus (Fr.) Gilb. & Budd.
Phellinus ferruginosus (Fr.) Pat.
Polyporaceae
Bjerkandera adusta (Fr.) Karst.
Coriolus hirsutus (Fr.) Quél.
C. pubescens (Fr.) Quél.
C. velutinus (Fr.) Quél.
C. versicolor (Fr.) Quél.
Coriolopsis gallica (Fr.) Ryv.
Daedaleopsis confragosa (Fr.) Schroet.
Fomes fomentarius (Fr.) Kickx
Fomitopsis pinicola (Fr.) Karst.
Gloeophyllum protractum (Fr.) Imaz.
G. sepiarium (Fr.) Karst.
Hirschioporus laricinum (Karst.) Teram.

Irpex lacteus (Fr.) Fr.
Lenzites betulina (Fr.) Fr.
Polyporus brumalis Fr.
Piptoporus betulinus (Fr.) Karst.
Poronidulus conchifer (Schw.) Murr.
Pycnoporus cinnabarinus (Fr.) Karst.
Roseofomes cajanderi (Karst.) Aosh.
Trichaptum abietinum (Fr.) Ryv.
T. pargamenum (Fr.) Ryv.
T. subchartaceum (Murr.) Ryv.
Porotheleaceae
Cyphellopsis anomala (Fr.) Donk
Solenia candida Pers.
Punctulariaceae
Phaeophlebia strigoso-zonata (Schw.)
W. B. Cooke
Schizophyllaceae
Schizophyllum commune Fr.
Stereaceae
Aleurodiscus amorphus (Fr.) Schroet.
Laxitextum crassum (Lev.) Lentz
Stereum hirsutum (Fr.) S.F. Gray
S. ostrea (Fr.) Fr.
Thelephoraceae
Thelephora cuticularis Berk.
Jelly Fungi
Dacrymycetaceae
Calocera cornea (Fr.) Fr.
C. viscosa (Fr.) Fr.
Femsjonia pezizaeformis (Lev.) Karst.

Guepiniopsis alpinus (Tracy & Earle)
Brasf.
Tremellaceae
Exidia glandulosa Fr.
E. nucleata (Schw.) Burt.
Myxarium hyalinus (Pers.) Donk
Pseudohydnum gelatinosum (Fr.) Karst.
Tulasnellaceae
Tulasnella lactea Bourd. & Galz.
Gasteromycetes
Astraeaceae
Astraeus hygrometricus (Pers.) Morg.
Geastraceae
Geastrum triplex Jungh.
Lycoperdaceae
Lycoperdon molle Pers.
L. norvegicum Demoul.
L. perlatum Pers.
L. pyriforme Pers.
Nidulariaceae
Crucibulum laeve (Rehn.) Kamb.
Sclerodermataceae
Scleroderma flavidum Ellis & Everh.
S. macrorhizon Chev.
DEUTEROMYCOTINA
Moniliaceae
Cladobotryum varium (Nees) Steud.
C. verticillatum (S.F. Gray) Hughes
Rhinotrichella globulifera deHoog
Tubercularia vulgare Fr.

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SUMMER DROUGHT EFFECTS ON THE GROWTH OF MATURE BALSAM FIR TREES

Allan P. Drew* and Edward J. Alyanak

School of Forestry and Wood Products
Michigan Technological University
Houghton, 49931

Balsam fir (*Abies balsamea*) is an important component of the boreal forest of Canada, as well as the northern hardwoods zone of the eastern deciduous forest. It occurs throughout the Upper Peninsula of Michigan and the northern half of lower Michigan and Wisconsin. A small to medium-sized tree, 40—60 feet in height and 16—18 inches in diameter, balsam fir occurs scattered or in mixture with other northern species (Harlow et al., 1979). It is extremely shade-tolerant and, although responding well to release, often spends much of its life beneath the overstory of taller trees (Fowells, 1965). The species' superficial root system, rarely penetrating deeper than 2 to 2.5 feet (Bakuzis & Hansen, 1965), predisposes it to potential growth reduction from drought, especially on xeric sites. Because of this, balsam fir normally grows better under moister site conditions than many other regionally important trees. Bakuzis & Hansen rated balsam fir at 3.6 on relative synecological moisture coordinates ranging from 1 to 5 for dry to wet site-adapted species. Of four species of *Abies,* balsam fir exhibits the greatest negative effect of water stress on photosynthesis, with rate reductions of 80% occurring as plant water potential falls to -12.4 bars (Puritch, 1973). The species is relatively drought-avoidant, but early stomatal closure limits potential photosynthate production under dry conditions.

Throughout the Upper Peninsula the summer of 1976 was extremely dry, with lower than average precipitation during the growing season. In early 1978, we studied the effect that the severe summer drought had had on annual growth ring and needle development in mature balsam fir trees growing on a xeric site.

A mixed conifer stand on a site representing a transition between *Acer-Quercus-Vaccinium* and *Tsuga-Maianthemum-Vaccinium* habitat types (Alyanak, unpubl.) and containing balsam fir as a component was chosen. Located north of Baraga, Michigan, along U. S. Highway 41 and adjacent to Lake Superior, the stand grew on sandy soil marking a former beachline. The soils were classified as Rubicon soils which are sandy, mixed, frigid of the Entic Haplorthods, with weakly expressed A2 and thin (6—8 cm) B2lir horizons and parent materials composed of medium sands. Rubicon soils have very low available water capacity with very rapid permeability and low natural fertility (Berndt, 1977).

Dominant and codominant overstory species of the seral community included red pine (*Pinus resinosa*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), and bigtooth aspen (*Populus grandidentata*) in diminishing order of importance. Several large jack pines (*Pinus banksiana*) and white pine (*Pinus strobus*) and balsam fir were also present.

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*Present address: College of Environmental Science and Forestry, State University of New York, Syracuse, 13210.

Balsam fir was the most numerous understory species, also occurring as an intermediate along with red maple and aspen, a senile species.

Twenty-four balsam fir trees ≥ 8.9 cm DBH were cored with an increment borer at breast height, and the growth rings, for 1973 through 1977, were measured on the cores to the nearest 0.1 mm. Two branch ends for each tree at breast height, 180 degrees apart and randomly oriented as to cardinal direction, were selected as sample points. Two needles, from the center and underside of each year's growth along each branch were removed and measured for length to the nearest 0.1 mm. All needles were dried at 70°C for 48 hours, then weighed on an analytical balance.

Weather data were obtained from annual summaries for the state which included monthly reports of temperature and precipitation for a Baraga 5 WNW reporting station (U. S. Dept. Commerce NOAA, 1972–78). In assessing the effects of past and current climate, least squares regression was used to examine the relationship of ring widths, needle length and weight, and growing season precipitation. Correlation coefficients were calculated for each biologically meaningful comparison.

Phenological changes during the early growing season in local balsam fir include bud swell and the beginning of shoot elongation in May, as well as the start of cambial activity. Buech (1976) reported that mature balsam fir growing near Rhinelander, Wisconsin, initiated shoot elongation in mid-May; elongation was 80% complete by the end of June and terminated in late July. The 127-day frost-free season at Rhinelander compares favorably with 135 days at Baraga. Although Baraga is north of Rhinelander, it has a slightly longer growing season due to the ameliorating effect of Lake Superior. It is likely that phenological events occur similarly in time at the two locations. In northern Minnesota, cambial activity of balsam fir begins in late May and is complete by early September (Ahlgren, 1957). In balsam fir and other northern conifers, leaves are formed as primordia in resting buds in the year prior to shoot elongation. Powell (1974) reported that in lateral buds of balsam fir growing in New Brunswick, production of needle primordia starts in late July and continues until October.

Table 1 shows 1976 to have been a very dry year, with less than half the normal May-September precipitation. Temperature variation between 1972 and 1978 was not appreciable, owing in large part to the moderating effect of Lake

TABLE 1. Annual climatic data for the Baraga 5 WNW, Michigan, Recording station for 1972–78. Shown are total annual and growing season precipitation, as well as mean annual and growing season temperature averaged monthly. E—wholly or partially estimated; M—one or more days record missing.

	Total Precipitation (in.)	May-September Precipitation (in.)	Mean Temperature (°F)	Mean Temperature May-September (°F)
1972	41.53	20.00	36.5	56.8
1973	36.86	19.56	41.4	58.1
1974	33.94	16.91	38.7 M	56.6 M
1975	38.24	16.32	40.8	60.0
1976	30.38	8.28	39.3 M	58.8 M
1977	37.02 E	18.28	40.4 M	59.3 M
1978	35.23 E	23.32	39.1 M	59.0

TABLE 2. Annual growth statistics of balsam fir for the years 1973–77. Shown are mean ring width (mm), leaf length (mm), and leaf weight (mg), along with standard errors.

	Mean Ring Width (mm)	Standard Error	Mean Leaf Length (mm)	Standard Error	Mean Leaf Weight (mg)	Standard Error
1973	1.9	0.117	19.8	0.550	——	——
1974	1.9	0.114	19.9	0.519	4.46	0.175
1975	1.7	0.350	20.2	0.408	4.39	0.154
1976	1.4	0.089	19.8	0.435	4.02	0.114
1977	1.5	0.069	14.8	0.678	2.74	0.181

Superior. Mean ring width of balsam fir trees was smallest in the drought year, 1976, but also small the following year (Table 2). Needle length and weight were lowest in 1977, with the latter showing some decline in 1976.

Regressions of ring width with the current or prior year's growing season (May-August) precipitation were not significant (Table 3). This lack of correlation is probably due to one year of drought resulting in two years of reduced radial growth (Zahner, 1968).

TABLE 3. Correlations between growth parameters of balsam fir and current and prior-year precipitation for selected months. The statistical significance of each correlation coefficient is represented as NS—not significant; * —5% level.

	Current Precipitation	Prior-Year Precipitation
Ring Width	May-August: $r = 0.77$ NS	May-August: $r = 0.71$ NS
Needle Length	May-July $r = -0.41$ NS	July-September: $r = 0.87$ NS
Needle Weight	May-July $r = -0.54$ NS	July-September: $r = 0.99$ *

Regressions of needle length or dry weight with current precipitation during needle development and growth (May-July) were not significant. However, the regression of needle dry weight with the prior year's July-September precipitation was significant at the .05 level. Needle length and the prior year's July-September precipitation were strongly related, with 76% ($r = .87$) of the variation explained by the regression. July-September precipitation of the prior year was used since this is the period when needle primordia are being formed in developing buds and reserve foods are accumulating.

A photograph of a typical lower crown balsam fir branch from a tree on the study site was taken in late 1979. Figure 1 shows reduced internode length in 1977 but little difference in shoot elongation between years before or after 1977. The effect of the dry summer of 1976 is seen in the following year's shoot length. Reduced number of needle primordia eventually limit shoot elongation regardless of how rapid the rate of growth may be (Garrett & Zahner, 1973).

Fig. 1. A lateral branch of balsam fir sampled following the 1979 growing season, showing reduced 1977 internode length in relation to growth in subsequent and prior years.
Fig. 2. A lateral branch of balsam fir showing abnormal 1977 needle development.

Although 1976 was dry, needle length was not affected, whereas xylem cell addition measured as ring width declined. The majority of leaf growth occurs in the month of June, which in 1976 was moist, with more than three inches of rainfall, with the remainder of the summer dry. Xylem cells were produced throughout the growing season and clearly showed reduction in numbers due to drought. Some reduction in needle weight, however, did occur in 1976. Schantz-Hansen & Joranson (1939) reported a similar phenomenon for balsam fir growing in Minnesota when, during the dry 1936 growing season, white, red, and jack pines showed considerably reduced needle length. They found that balsam fir, which completes shoot growth earlier than the pines, was able to take advantage of early spring soil moisture and produce slightly longer needles than in the prior year, even though total growing season moisture was 47% of normal.

As the productive capacity of old needles decreases, they become less efficient than new needles as energy sources for current growth (Loach & Little, 1973; Dickmann & Kozlowski, 1968; Clark, 1956). Since the number of needles comprising the 1977 growth was reduced by the prior year's drought, the capacity to produce carbohydrate to meet current demand was less. Loach & Little (1973) showed that in June, in New Brunswick, current year's foliage, as well as that of the past year, are a prime source of photosynthate for cambial growth of the prior year's shoot. Early in the growing season, the new shoot

relies upon food stores accumulated in last year's foliage from both past and current photosynthesis. Later, new foliage becomes more important than old as a source of photosynthate for cambial activity and new xylem cell addition to the shoot.

Needle growth in 1977 was less than in 1976, even though current precipitation was adequate in every month. The unexpectedly large reductions in needle length and weight are assumed to be related to reduced availability of carbohydrate rather than moisture stress. Olofinboba & Kozlowski (1973) have demonstrated the importance of carbohydrate reserves produced in the prior year to current shoot growth in red pine. Little (1974) showed the importance of current growth products to current shoot growth in balsam fir but found that carbohydrate produced and accumulated just prior to spring bud break does not affect subsequent shoot growth. Garrett & Zahner (1973) found reduced needle length in red pine around which moisture was excluded. This was related, first of all, to low available moisture during the current growing season. Second, ample moisture in the prior year resulted in large numbers of primordia being formed in buds which ultimately produced many needle fascicles, but shorter needles. In our study, neither of these factors was present to explain why shorter needles were produced in 1977, a wet year. It is likely that carbohydrate availability exerted a greater influence than moisture stress upon needle growth.

Carbohydrate production and storage during 1976 was curtailed at a low level by the drought, as expressed by reduced ring growth in that dry year and limited new shoot growth the following year. From the standpoint of reserve carbohydrate supply or current productive capacity, there were limitations on tree growth during 1977, manifested not only by needle length and weight reductions but also by decreased xylem formation. The latter is often affected by current climate; but in this case the extreme drought of the prior year also had a limiting effect. Fritts (1976) has shown high correlations between climate of the prior year and current ring width growth for a number of semi-arid site conifers.

Some further increase in the length and weight of 1977 foliage may have occurred during the 1978 growing season but was not assessed. Morris (1951) found that during the second growing season, the needles of balsam fir increase about 8% in length and 20% in weight. Allowing for these corrections, 1977 needle development was still markedly reduced.

Some trees showed twisted and curled needles on 1977 shoot internodes (Figure 2), reflecting a probable drought effect on primordia formation or damage to new primordia during late 1976. This feature was not observed in needles emerging from buds formed in any other than the 1976 drought year. Jackson (1948) and Parris (1967) reported examples of "needle curl" in shortleaf and loblolly pines caused by abnormal fascicular sheath development under conditions of low soil moisture and high air temperature, respectively. Needle curl in balsam fir, which does not have needles in fascicles enclosed by a sheath, seems to indicate that buds formed under moisture stress have a lessened potential for normal growth the following year. This reduced growth potential may result in a combination of abnormal needle development and reduced shoot growth.

We conclude that the most damaging effects of summer drought to balsam fir growing on sandy sites may be to early bud development when needle primordia are being formed. Reduction of photosynthetic surface area the following summer, both in terms of number and size of needles, limits productive capacity and annual ring width increase, even though current climate may otherwise favor rapid growth. A secondary effect may act through availability of stored food reduced during the dry year.

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A KEY TO GRASSHOPPER FOOD PLANTS
BASED ON ANATOMICAL FEATURES

M. L. Nelson and S. K. Gangwere

Dept. of Biological Sciences
Wayne State University
Detroit, Michigan, 48202

The food plant selection of Orthoptera has been investigated in a number of ways. Aside from the classic technique of field observation to determine diet and preferences, the common methods include differential feeding tests of captured individuals (e.g., Isely, 1941, 1944, 1946; Gangwere, 1961), analysis of structural adaptations of mouthparts (Isely, 1944; Gangwere, 1961, 1965; Chapman, 1964), morphological studies on the alimentary canal (Gangwere, 1966; Tyrkus, 1971), and analysis of the morphology of feculae (Frost, 1928; Gangwere, 1961, 1962, 1969; Tyrkus & Gangwere, 1970). These techniques allow for categorizing species or taxonomic groups according to gross diet. Microscopic analysis of crop contents, suggested by Isely & Alexander (1949), has been performed by Mulkern & Anderson (1959), Gangwere (1961), Mulkern et al. (1962, 1969), and Ueckert (1968), among others. This technique has proven useful, and it seems possible to construct a key to the food plants of a given flora based on epidermal characteristics. Such a key could provide a quick, precise diet determination from the gut contents of any phytophagous animal, insect or vertebrate.

Our key is not the first. Brusven & Mulkern (1960) devised a dichotomous key using epidermal characteristics to identify a limited assortment of Great Plains forbs, grasses, and sedges, but it failed to differentiate many plants at the species level. (In fact, they listed 25 species under one couplet.) Their key, though interesting, has restricted applicability, particularly with regard to a northeastern flora. Therefore, it remains to be determined if it is possible to develop an accurate, usable key to an extensive flora. Toward this end, a mixed grass-herbaceous field in Michigan was investigated, and previously unused epidermal characteristics were employed to take determinations to species level.

During the field seasons of 1963, 1964, and 1965, a vegetational analysis was conducted on a mixed grass-herbaceous field, Evans Old Field, at the E. S. George Reserve, Pinckney, Michigan.[1] Plants were collected, identified, and fed separately to various acridid grasshoppers common in Michigan, thus producing known crop contents and feculae. The animals and a reference collection of plants were stored separately in labeled vials containing 70% ethyl alcohol, while the defecated feculae were stored individually in dry, labeled vials. Microscope slides were made of these materials. In making slides of crop contents, the heads of the preserved grasshoppers were pulled free; the crop contents forced out

onto the slide and teased apart while adding several drops of 70% ethyl alcohol; CMC−10 mounting medium applied; and a cover-slip added. The slides of feculae were made by moistening fecal pellets with either 70% ethyl alcohol or water, teasing them apart, and mounting them as above. Simulated crop content slides were made using Mulkern & Anderson's technique (1959), which chops fresh or preserved plants in a micro-assembly blender into a particle size approximating that found naturally in acridid crops. Again, these materials were mounted in CMC−10 medium. Finally, confirmatory feculae slides for each plant studied were made using the previously described fecular technique, substituting CMC−9 (stained) mounting medium for the CMC−10. After preliminary drying, all slides were ringed with clear nail polish to prevent medium withdrawal.

For purposes of the key, the plants examined were restricted to 47 species with a frequency of 5% or above in Evans Old Field. Each species frequency was calculated by dividing the random number of plant samples with this particular species in it by the total number of plant samples. (Plants with frequencies below 5% can be considered negligible in the diet of grasshoppers, and so were not used.) Though crop contents and feculae from several Old Field grasshopper species were available, the present investigation was restricted to one species, *Melanoplus confusus* Scudder. Use of a single species proved adequate, because pilot comparisons of crop and fecal materials from several different grasshopper species fed on the same plants showed no cellular differences from those associated with *M. confusus*. That is, using different grasshoppers seemed to make no difference in the final anatomical appearance of the plant foods.

All slides were scanned by a binocular phase contrast microscope at a magnification of 150, and relevant structures were then examined in greater detail at 300, 675, and 1500 power. Morphology, size, and abundance of the following features were recorded for each plant species in the hope that they would be diagnostic: guard cells; subsidiary cells; trichomes; unspecialized epidermal cells; crystals; and pollen grains. (Of these, only the first four are epidermal.)

A pair of guard cells flanks each of the stomata. Various numbers of subsidiary cells often surround the guard cells and may form a distinctive pattern. Trichomes are plant hairs. The unspecialized epidermal cell type was taken primarily from the leaves' lower epidermis, which usually has more stomata than the upper. Davies (1959) described crystal precipitation from the epidermal cells of some species whose tissues were teased apart in alcohol or water at 55°C and noted that crystals do not appear when the same plants are mounted in cold water. Pollen grains are often diagnostic. Gross slide color and other epidermal structures, if consistent, were also recorded in the hope that they would be useful. Color was observed by viewing the slide against a white background one day after mounting.

Slide co-ordinates of the clearest, most representative structures were recorded for photographic purposes. They were photographed with a 35 mm camera through the phase microscope, printed on 5 × 7 in. black-and-white paper, and copied on tracing paper to enhance clarity. The tracings were re-photographed in page form and then photographically reduced to 8 × 10 in. prints.

FIGURE A (in 2 plates). Unicellular Trichomes. 1. Bristle trichomes on vein epidermis of *Poa compressa*, ×114. 2. Unicellular, elongate trichome of *Poa pratensis*, ×257. 3. Unicellular, elongate trichome of *Danthonia spicata*, ×57. 4. Smooth, pointed, broad-based trichome of *Oxalis stricta*, ×114. 5. Rough, blunt, contracted based trichome of *Oxalis stricta*, ×257. 6. Blunt, short, rough-walled trichome of *Lepidium virginicum*, ×570. 7. Stout, rough-walled, widened based trichome of *Daucus carota*, ×257. 8. Stout, rough-surfaced, widened based trichome of *Daucus carota*, ×57. 9. Tip of trichome from figure A8 of *Daucus carota*, ×257. 10. Elongate, irregular surfaced trichome of *Lechea villosa*, ×114. 11. Recurved tip (uncinate) trichome of *Galium pilosum*, ×114. 12. Curved trichome of *Galium pilosum*, ×114. 13. Elongate, smooth, widened square-based trichome of *Potentilla intermedia*, ×257. 14. Elongate, smooth trichome of *Rubus flagellaris*, ×114.
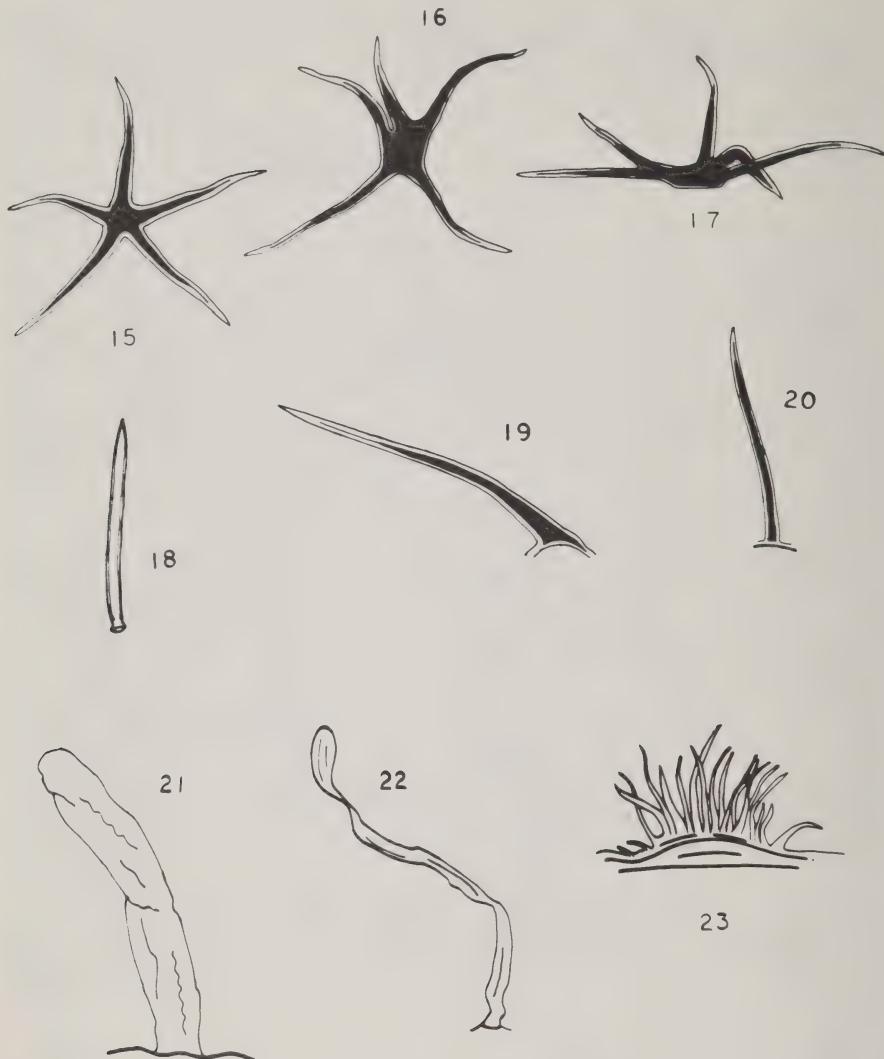
FIGURE A (continued). Unicellular Trichomes. 15. Surface view of symmetrical multi-arm (stellate) trichome of *Hieracium gronovii*, ×257. 16. Surface view of asymmetrical multi-arm trichome of *Hieracium gronovii*, ×257. 17. Side view of asymmetrical multi-arm trichome of *Hieracium gronovii*, ×257. 18. Elongated, pointed, bulbous base type trichome of *Hieracium gronovii*, ×114. 19. Elongated, pointed, widened base trichome of *Verbena* sp., ×114. 20. Elongated, pointed trichome of *Carya* sp., ×114. 21. Thin walled, blunt, "balloon" trichome of *Arctium minus*, ×257. 22. Thin walled, blunt, "balloon" trichome of *Arctium minus*, ×95. 23. Cluster of smooth, pointed trichomes of *Arctium minus*, ×106.

ANATOMICAL KEY TO OLD FIELD PLANT SPECIES

1. Stomata appearing banded from radiating ridges of overlapping subsidiary cells; scalloped fragments common (figs. C1, E1) · · · · · · · · · · · · · · · *Equisetum arvense*
   Stomatal guard cells not as above (figs C2–12) 2
2. Stomatal guard cells appear "plugged" at apices because of invaginations of subsidiary cell walls (fig. C2) . . . . *Juniperus communis*
   Stomata guard cells not as above (figs. C3–12) 3
3. Lower epidermal cells rectangular with undulating walls; bristle trichomes common on vein epidermis (figs. A1, D1–5) 4
   Lower epidermis not as above; bristle trichomes not common on vein epidermis (figs. D6–12) 9
4. Epidermis, both vein and intervein, without cork cells or silica-cork "couples" (fig. D1)–Family Cyperaceae . . . . *Cyperus filiculmis*
   Epidermis, both vein and intervein, often with cork cells and silica-cork "couples" (fig. D2)–Family Poaceae 5
5. Stomatal subsidiary cells' outer walls usually parallel (fig. C3)–Genus *Poa* 6
   Stomatal subsidiary cells expanded with outer walls protruding, often approaching a triangular shape (figs. C4–6) 7
6. Vein epidermis with long cells alternating irregularly with bristles; unicellular, elongate trichome with wide "slot" base (figs. A2, D3) . . . . *Poa pratensis*
   Vein epidermis with long cells alternating regularly with bristles or rectangular short cells; unicellular, elongate trichome with wide "slot" base not present (fig. D4) . . .
   . . . . *Poa compressa*
7. Epidermis often with intervein cell differentiation (fig. D5) . . . . *Panicum oligosanthes*
   Epidermis without intervein differentiation (figs. D1, D2) 8
8. Unicellular, elongate trichomes common (fig. A3) . . . . *Danthonia spicata*
   Unicellular, elongate trichomes not common . . . . *Aristida purpurascens*
9. Trichomes absent or not common 10
   Trichomes common (figs. A4–23, B1–33) 15

Trichomes Not Common

10. Lower epidermal cells regular in shape (figs. D6, 7, 11) 11
    Lower epidermal cells irregular or sharply wavy (figs. D9, 10, 12) 13
11. Lower epidermal cells consisting of elongate rectangles; cell size average; cross-hatched cells often present (figs. D6, E3) . . . . *Chrysanthemum leucanthemum*
    Lower epidermal cells not as above; cross-hatched cells not present (figs. D7, 11) . . 12
12. Lower epidermal cells regular-robust; cell size average (figs. D11, E2, 5)* . . . . . .
    . . . . *Tragopogon pratensis*
    Lower epidermal cells polygonal in shape; cell size large (fig. D7) . . *Rumex acetosella*
13. Lower epidermal cells sharply wavy (fig. D9) . . . . *Lactuca* sp.
    Lower epidermal cells irregular in shape (figs. D10, 12) 14
14. Stomata usually with 4 subsidiary cells; convoluted cells often present; prepared fragments red-brown (figs. C7, E4) . . . . *Plantago rugelli*
    Stomata usually with 2 or 3 subsidiary cells; convoluted cells absent; prepared fragments light-yellow (fig. C8) . . . . *Hypericum perforatum*

Trichomes Common

15. Unicellular trichomes common (figs. A4–23) 16
    Multicellular trichomes exclusively (figs. B1, 2, 7–33) 27
16. Unicellular trichomes exclusively (figs. A4–18, 21–23) 17
    Both unicellular and multicellular trichomes present (figs. A19, 20, B3–6) 25
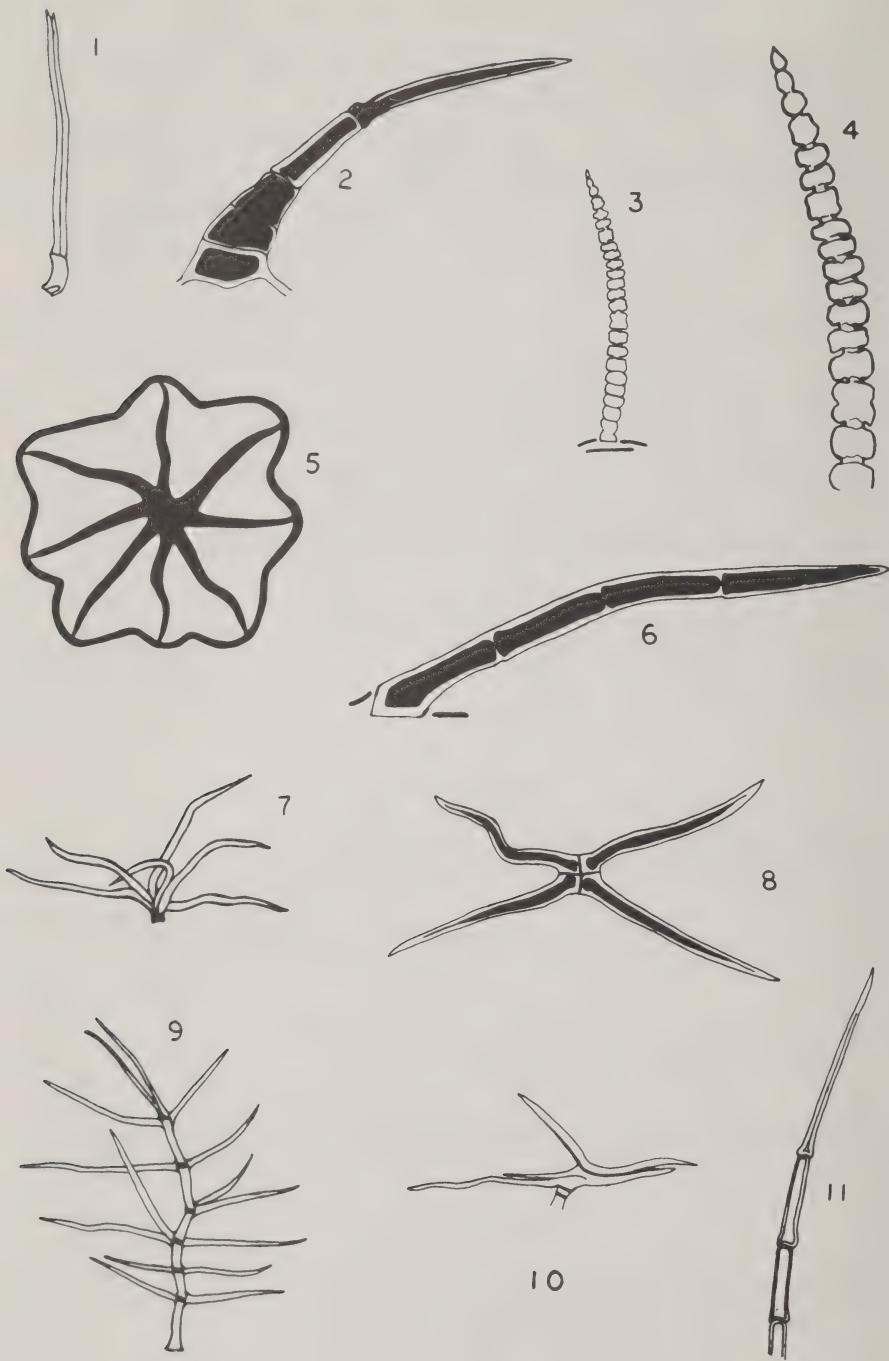
FIGURE B (in 3 plates). Multicellular Trichomes. 1. Paired vertical shaft trichome of *Erigeron strigosus*, ✕257. 2. Stout, jointed trichome of *Erigeron Strigosus*, ✕257. 3. "Bead-like" trichome of *Verbena* sp., ✕114. 4. Tip of trichome from figure B3 of *Verbena* sp., ✕257. 5. Surface view of peltate trichome of *Carya* sp., ✕554. 6. Linear trichome of *Monarda fistulosa*, ✕257. 7. Side view of six-armed trichome of *Helianthemum canadense*, ✕114. 8. Surface view of four-armed trichome of *Helianthemum canadense*, ✕257. 9. Branched trichome of *Verbascum thapsus*, ✕57. 10. Trichome with asymmetrically-armed terminal cell of *Hieracium longipilum*, ✕114. 11. Pinched-joint trichome of *Liatris aspera*, ✕114.

Unicellular Trichomes

17. Two types of trichomes common (figs. A4, 5, 15–18, 21–23) 18
    One type of trichome common (figs. A6–14) 20
18. Trichomes symmetric- to asymmetric-stellate (multi-arm type) and elongate, pointed type with bulbous base (figs. A15–18, E7)** . . . . *Hieracium gronovii*
    Trichomes not as above (figs. A4, 5, 21–23) 19
19. Trichomes smooth-walled, pointed type with expanded base and rough-walled, blunt type with contracted base (figs. A4, 5) . . . . *Oxalis stricta*
    Trichomes thin-walled, blunt, "balloon" type, often appearing only partially "in-flated," and smooth, pointed type, usually in clusters; alternating cells often present (figs. A21–23, E8) . . . . *Arctium minus*
20. Trichomes blunt, short; wall surface rough (fig. A6) . . . . *Lepidium virginicum*
    Trichomes pointed, longer; wall surface rough or smooth (figs. A7–14) 21
21. Trichome wall surface irregular to rough; trichome body slightly curved (figs. A7–10) 22
    Trichome wall surface smooth; trichome body curved to recurved or wavy (figs. A11–14) 23
22. Trichomes stout; surface rough; base widened (figs. A7, 8, 9) . . . . *Daucus carota*
    Trichome elongate; surface irregular; base not conspicuously widened but often darkened; base orange under brightfield illumination (fig. A10) . . . . . *Lechea villosa*
23. Trichomes usually recurved at tip; sometimes trichome merely curved, base normal; stomatal subsidiary cells parallel to guard cells; nuclei often conspicuous in all cell types (figs. A11, 12, C9) . . . . *Galium pilosum*
    Trichomes usually long and smooth, sometimes wavy; base conspicuously darkened or refractive; stomatal subsidiary cell pattern variable; nuclei usually not conspicuous (figs. A13, 14) 24
24. Trichomes usually tortuous; thick walls obvious under brightfield illumination; square base often conspicuously wider than lower body of trichome; prepared frag-ments green-brown (fig. A13) . . . . *Potentilla intermedia*
    Trichomes usually straight to curved; thick walls inconspicuous under brightfield illumination; square base with rounded corners and not much wider than lower body of trichome; prepared fragments dark-brown to black (fig. A14) . . . . *Rubus flagellaris*

Unicellular And Multicellular Trichomes

25. Multicellular trichome "bead-like"; unicellular trichome elongate, pointed, with widened base (figs. B3, 4, A19) . . . . *Verbena* sp.
    Trichomes not as above (figs. B5, 6, A20) 26
26. Multicellular trichomes peltate, usually with 8 arms; unicellular trichomes elongate, pointed, base not widened (figs. B5, A20) . . . . *Carya* sp.
    Trichomes linear with ca. 1 to 8 cells (fig. B6) . . . . *Monarda fistulosa*
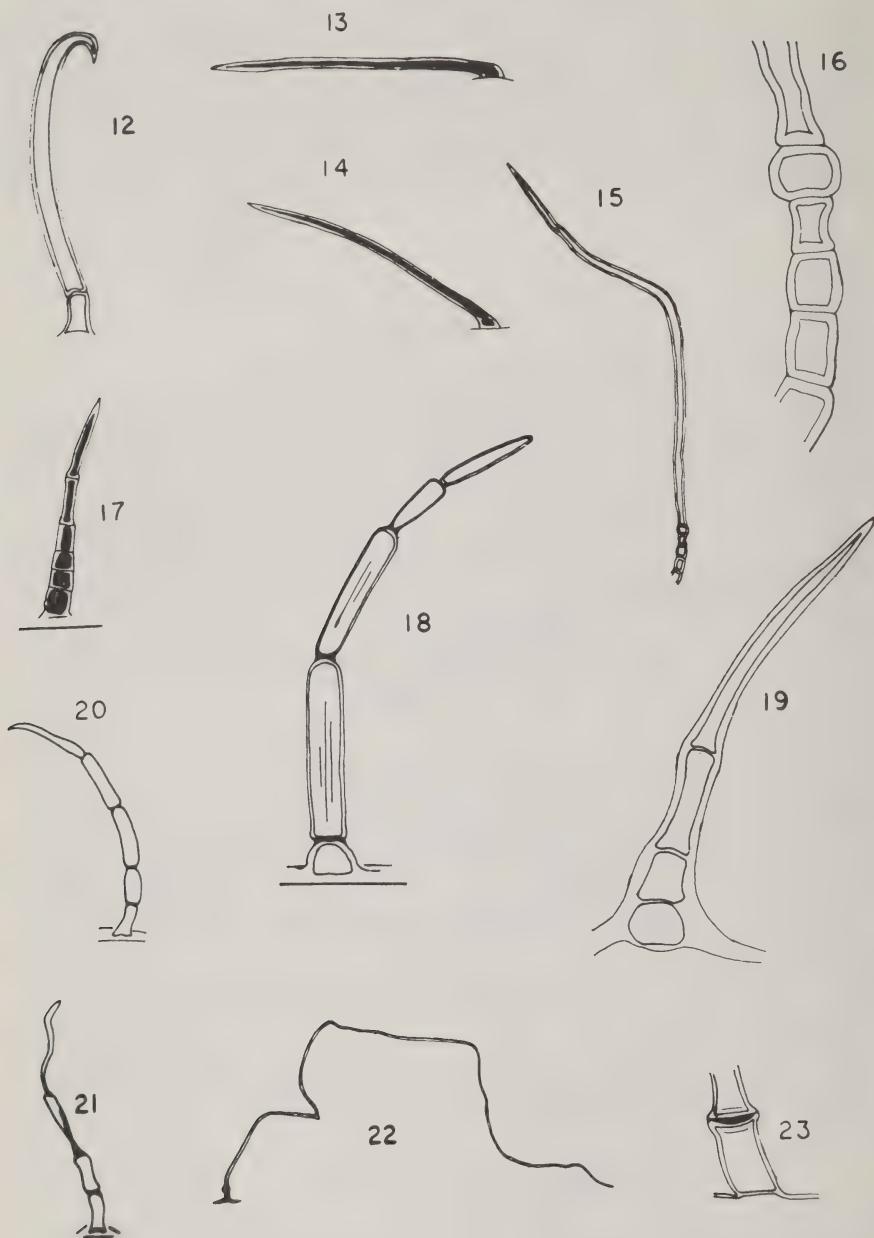
FIGURE B (continued). Multicellular Trichomes. 12. Curved tip trichome of *Desmodium illinoense*, ×257. 13. Curved base of *Lespedeza capitata*, ×114. 14. Curved base trichome of *Lespedeza hirta*, ×114. 15. Extremely elongate terminal cell trichome of *Achillea millefolium*, ×114. 16. Base of trichome from figure B15 of *Achillea millefolium*, ×257. 17. Stout, smooth, pointed tipped trichome of *Quercus* sp., ×114. 18. Pinched-joint trichome of *Physalis heterophylla*, ×114. 19. Stout, pointed trichome of *Physalis heterophylla*, ×257. 20. Pinched-joint trichome of *Asclepias syriaca*, ×114. 21. Pinched-joint trichome with partially collapsed cell of *Asclepias syriaca*, ×114. 22. Extremely elongate terminal cell trichome of *Antennaria neglecta*, ×57. 23. Base of trichome from figure B22 of *Antennaria neglecta*, ×570.

Multicellular Trichomes

FIGURE B (continued). Multicellular Trichomes. 24. Expanded-joint, pointed, often tuberculated trichome of *Ambrosia artemisiifolia*, ×114. 25. Base of trichome from figure B24 of *Ambrosia artemisiifolia*, ×257. 26. Stout trichome of *Solidago nemoralis*, ×257. 27. "Whip" trichome of *Solidago nemoralis*, ×525. 28. Linear trichome of *Solidago rigida*, ×114. 29. Short, whip-shaped trichome of *Solidago rigida*, ×570. 30. Linear trichome of *Solidago juncea*, ×257. 31. Two-celled linear trichome of *Leonurus cardiaca*, ×257. 32. Six-celled linear trichome of *Leonurus cardiaca*, ×57. 33. Elongate, smooth, expanded-joint trichome of *Plantago artistata*, ×57.

40. Trichomes often with expanded joints, pointed tip, and elongate cells present (figs. B24, 25, 33) 41
Trichomes often with pinched joints, blunt tip, and occasional collapsed cells present (figs. B11, 18–21) 42
41. Trichomes with dilated joints, elongate, usually smooth; stomatal subsidiary cells overlapping (figs. B33, C12) . . . . *Plantago aristata*
Trichomes with dilated joints, wall surface often tuberculate; stout, ca. 3-celled trichomes also present; stomatal subsidiary cell pattern varying (figs. B24, 25) . . . .
. . . . *Ambrosia artemisiifolia*
42. Trichomes with pinched joints; stout, pointed trichome also present; lower epidermis sharply wavy to irregular, unwrinkled; prepared fragments light green-brown (figs. B18, 19, D9, 10, 12) . . . . *Physalis heterophylla*
Not as above (figs. B11, 20, 21, D8) 43
43. Trichomes large; lower epidermis irregular, unwrinkled; color of prepared fragments varying (figs. B20, 21, D10, 12) . . . . *Asclepias syriaca*
Trichomes smaller; lower epidermis irregular to regular, wrinkled; prepared fragments usually very dark (figs. B11, D8, E7)** . . . . *Liatris aspera*
44. Trichomes exclusively stout, smooth, with pointed tip: lower epidermis regular-robust (figs. B17, D11) . . . . *Quercus* sp.
Trichomes approximately 2- and 6-celled, linear, usually tuberculate; lower epidermis sharply wavy (figs. B31, 32, D9) . . . . *Leonurus cardiaca*

*pappus bristles noted (figs. E2, 5)
**pappus bristles with unusually long projections noted (fig. E7)

Variations were noted in the slide preparations. As observed by Mulkern & Anderson (1959) and confirmed in this study, simulated crop contents made from plant materials chopped in a blender produce slides generally superior to those made from actual crop contents. This suggests that data based on simulated contents could give an erroneous impression of what can be observed from analysis of crop contents or fecal materials. Therefore, all characters used in the key were checked with confirmatory slides of feculae, which proved either equal or only slightly inferior to actual crop content slides. Slides mounted in CMC–9 (stained) medium were essentially the same as those in the CMC–10 (clear) medium, except when using brightfield, in which the former displayed a perceptible increase in contrast.

Esau (1965) reported that variation in epidermal cells occurs at different areas on the leaf and during different stages of development. Variation also occurs between plants of the same species found at different locations. Therefore, an attempt was made to find key structures that were both common and consistent. Sometimes a compromise proved necessary, and a dominant structure type had to be chosen. Characters other than those listed (e.g., a specific type of trichome) may also be present, but to a lesser degree.

The several structures used in the key exhibit different degrees of usefulness. The trichomes, or plant hairs, proved to be the most useful of the characters because they are common, and, according to Esau (1965), appear in early plant development and tend to persist. (If ephemeral, that condition would have been detected through previous slide examinations). Brusven & Mulkern (1960) placed emphasis on trichome size. That character was used sparingly in our key because, in the plants studied, the dimension proved to be highly variable. Much greater consistency was obtained by comparing different
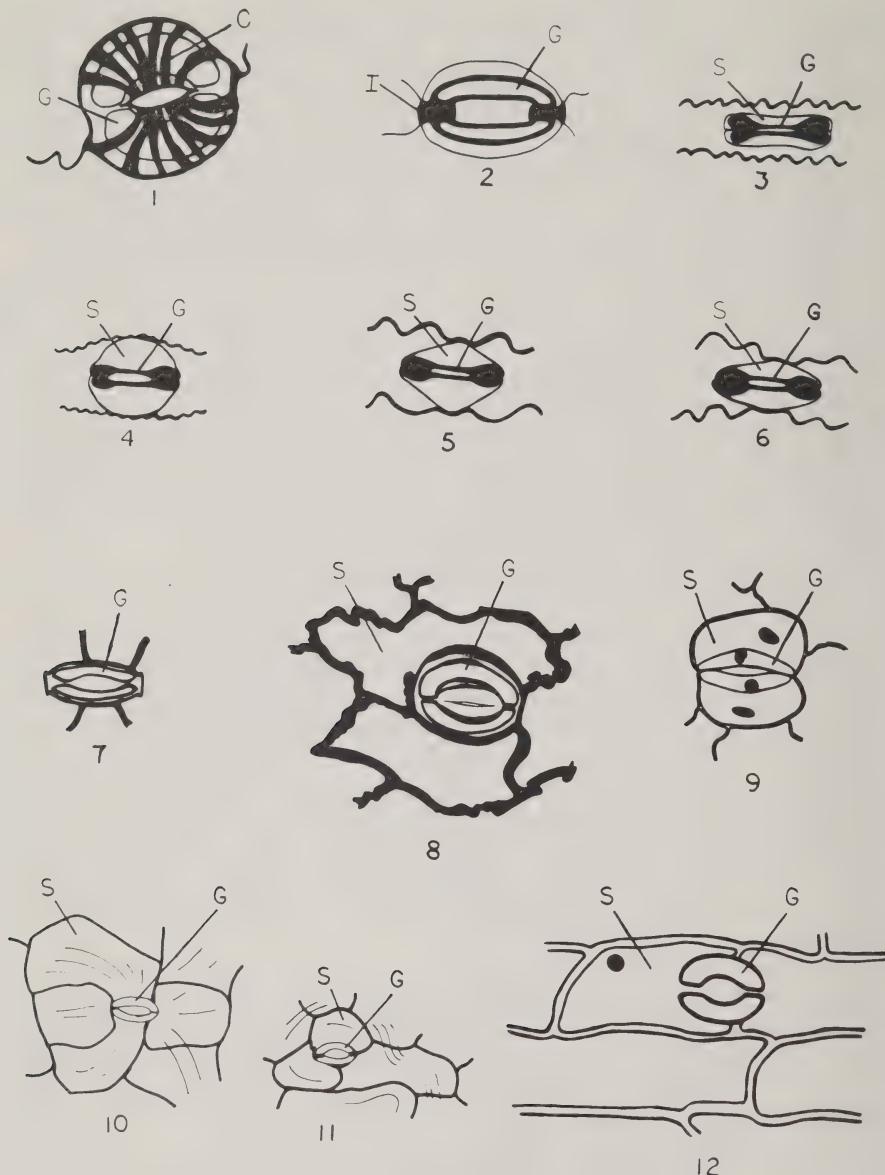
FIGURE C. Stomatal Types. 1. Guard cells of *Equisetum arvense* appearing "banded" because of overlapping, ridged subsidiary cells, ×557. 2. Guard cells of *Juniperus communis* appearing "plugged" because of invaginations of epidermis, ×554. 3. Stoma of *Poa compressa* with parallel-sided subsidiary cells, ×554. 4. Stoma of *Danthonia spicata* with protruding subsidiary cell walls, ×554. 5. Stoma of *Panicum oligosanthes* with protruding subsidiary cell walls, ×554. 6. Stoma of *Panicum oligosanthes* with slightly protruding subsidiary cell walls, ×554. 7. Stoma of *Plantago rugelli,* ×554. 8. Stoma of *Hypericum*

perforatum, ×570. 9. Stoma of *Galium pilosum* with paracytic subsidiary cell pattern (the long axis of the subsidiary cell is parallel to the long axis of the guard cell) and conspicuous nuclei, ×554. 10. Stoma of *Solidago rigida* with regular-robust, moderately wrinkled lower epidermis, ×257. 11. Stoma of *Solidago nemoralis* with regular-robust, smooth lower epidermis, ×257. 12. Stoma of *Plantago aristata* (Plantaginaceae) with diacytic subsidiary cell pattern (the long axis of the subsidiary cell is perpendicular to the long axis of the guard cell), ×554.—ABBREVIATIONS: O - overlapping ridges. G - guard cell. I - invagination. S - subsidiary cell.

trichome types (e.g., the 2-celled hair with recurved tip, fig. B12, as opposed to the 1-celled hair with recurved tip, fig. A11). The guard cells were found to be useful in some family separations (e.g., the Poaceae), while the subsidiary cells tended to be useful at a more specific level (fig. C). The unspecialized epidermal cells, usually of the lower epidermis, were used when consistent (fig. D). Gross slide color was rarely consistent, and, when it was, the character was used only as confirmatory. A number of other cellular features were used as confirmatory characters if diagnostic and consistent. Still other structures recorded during the research were not used at all. Among them are the crystals referred to by Davies (1959). Those observed in the present study proved to be inconsistent, and the expected correlations between crystals and type of slide preparation, either alcohol or cold water, did not materialize. Pollen grains were not observed frequently enough to be useful, and insect sclerites were only occasionally noted. Their reduced frequency and complexity of determination made inclusion unfeasible.

Pappus bristles, consisting of main axis and spikes, are common to many of the species studied (e.g., fig. E2, 5, 7). These bristles are noted as such when seen in a species. For purposes of the key, pappus bristles are not considered to be epidermal trichomes, either single or multi-cellular. Therefore, it is possible to have a species (e.g., *Tragopogon pratensis*) that falls into the section "Trichomes Not Common," yet pappus bristles may be common.

Species determination is problematical within several genera. The two species of *Lespedeza, L. hirta* and *L. capitata,* can be differentiated only by measuring the curvature of the trichome base cell which in itself may be variable (fig. B13, 14). Perhaps the gradations are explicable on the basis that these legumes are reportedly hybridizing in Evans Old Field, where the materials were collected. The grasses *Poa pratensis* and *P. compressa* are separated by the relative stability of certain cell sequences along the vein epidermis, as first noted by Metcalfe (1960), who listed the cytological characteristics of various *Poa* tissue types. These grasses are among the few plants in the key on which previous anatomical observations have been published. Finally, the three species of *Solidago* studied, *S. juncea, S. nemoralis,* and *S. rigida,* displayed variation in their "whip" trichome structures (fig. B27, 29). In keying the three it was necessary to use dominant types for all of the trichomes, as well as the subsidiary cell patterns.

CONCLUSIONS

Epidermal parts from 47 species of plant from Evans Old Field, E. S. George Reserve, Michigan, recovered from the crops or feculae of Orthoptera can be used for species identification.
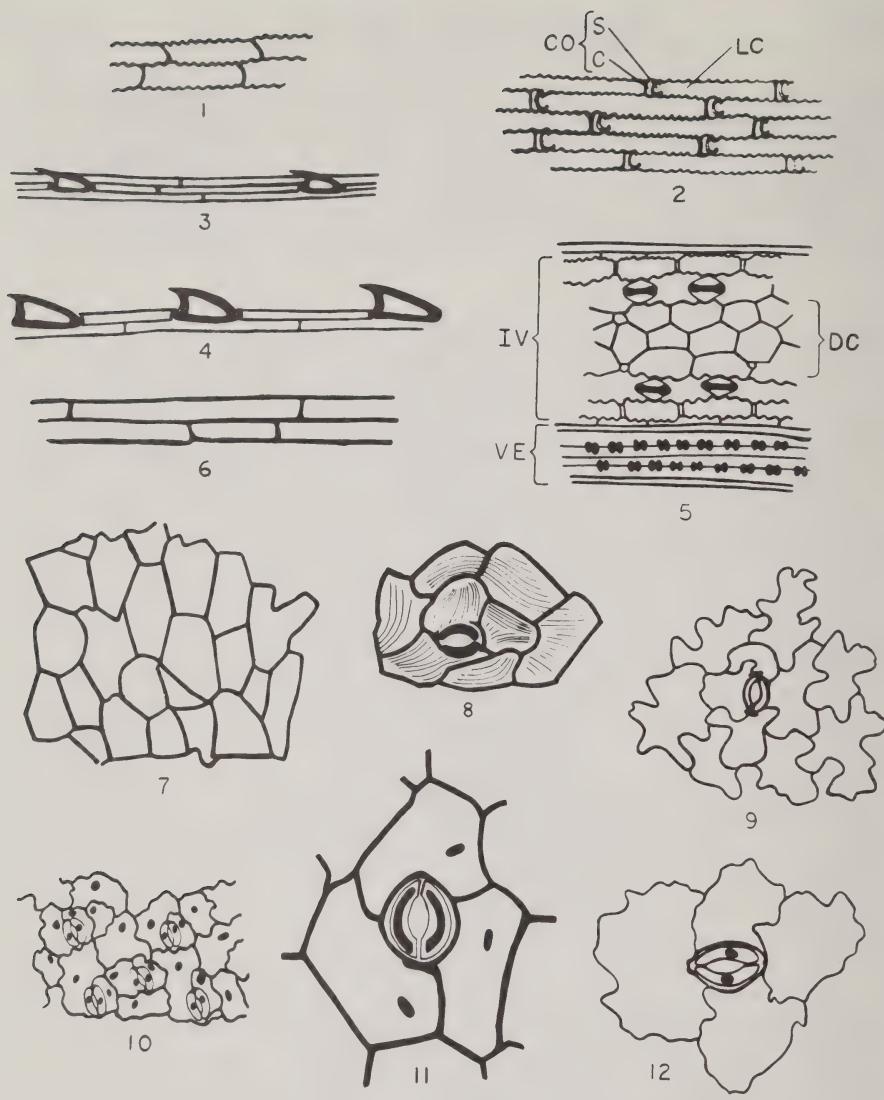
FIGURE D. Epidermal Cell Types. 1. Intervein lower epidermis of *Cyperus filiculmis,* ×257. 2. Intervein lower epidermis of *Poa compressa* with silica-cork "couples," ×257. 3. Vein epidermis of *Poa pratensis* with long cells alternating irregularly with teeth, ×257. 4. Vein epidermis of *Poa compressa* with long cells alternating regularly with teeth, ×257. 5. Lower epidermis of *Panicum oligosanthes* with polygonal differentiated cells in intervein region, ×225. 6. Lower epidermis of *Chrysanthemum leucanthemum* consisting of elongate rectangular cells, ×257. 7. Lower epidermis of *Rumex acetosella* consisting of polygonal cells, ×114. 8. Heavily wrinkled lower epidermis of *Solidago juncea* consisting of regular-robust cells, ×257. 9. Lower epidermis of *Lactuca* sp. consisting of wavy anticlinal cells, ×257. 10. Lower epidermis of *Hypericum perforatum* consisting of irregular-shaped cells, ×257. 11. Lower epidermis of *Tragopogon pratensis* consisting of regular-robust cells, ×570. 12. Lower epidermis of *Hieracium longipilum* consisting of irregular-shaped cells, ×510.—ABBREVIATIONS: C - cork cell. S - silica cell. CO - "couple." DC - differentiated cells. IV - intervein lower epidermis. LC - lower epidermal cell (unspecialized). VE - vein lower epidermis.
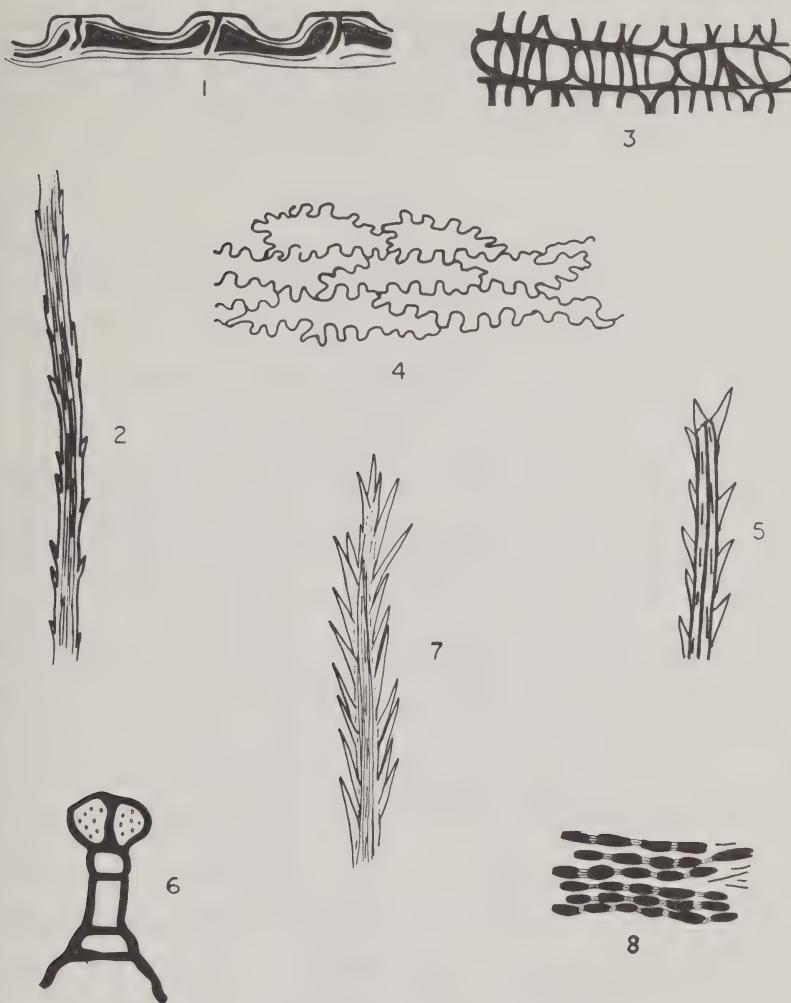
FIGURE E. Miscellaneous. 1. Scalloped fragments of *Equisetum arvense*, ×257. 2. Pappus bristles of *Hieracium longipilum*, ×111. 3. Cross-hatched cells of *Chrysanthemum leucanthemum*, ×501. 4. Convoluted cells of *Plantago rugelii*, ×257. 5. Pappus bristles of *Erigeron strigosus*, ×257. 6. Stalk gland of *Verbascum thapsus*, ×570. 7. Pappus bristles of *Liatris aspera* with elongate spikes, ×257. 8. Alternating cells of *Arctium minus*, ×257.

Microscopic determination of plant foods is a quick and accurate technique to ascertain food selection.

As expected, the most closely related plants are usually the most difficult to differentiate at the cellular level.

Based on abundance and consistency, the most useful microscopic characters are trichomes, stomatal complexes consisting of guard and subsidiary cells, and unspecialized epidermal cells. Pollen grains are also diagnostic but observed so infrequently in these preparations that they are not useful. Cell crystals were not found to be diagnostic.

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INTRODUCTIVE HYBRIDIZATION AND HABITAT SEPARATION IN LYCOPUS AMERICANUS AND L. EUROPAEUS AT THE SOUTHWESTERN SHORES OF LAKE ERIE

Mark E. Andrus and Ronald L. Stuckey

Dept. of Biology
Baldwin-Wallace College
Berea, Ohio, 44017

Dept. of Botany
The Ohio State University
Columbus, 43210

Analysis of plants of *L. americanus, L. europaeus,* and plants intermediate between the two species from populations at the southwestern end of Lake Erie suggests that introgressive hybridization has occurred. Evidence comes from an analysis of the shape of leaves, indumentum on leaves and stems, internodal lengths, and size and shape of nutlets. The data offer supportive evidence for introgressive hybridization as presented by Webber & Ball (1980), with whom we are in complete agreement. Our studies, like theirs, suggest that introgression is more toward *L. europaeus.* Field studies show that *L. americanus* generally occurs in drier sites, whereas *L. europaeus* and the intermediates grow in wetter sites. Compared with observations made by the second author ten years previously at the same localities, intermediates are now much more common, but because of apparent differences in habitat plants of *L. americanus* do not appear to be reduced in number.

Recently established populations of the non-indigenous *Lycopus europaeus* L., European water-horehound (Labiatae), on the southwestern shore of Lake Erie exhibit extreme variability. Sometimes it is difficult to distinguish the plants from the widespread, common native *L. americanus* Muhl., American water-horehound. Stuckey & Phillips (1970) suggested that the species were hybridizing. From studies of populations in southern Canada, Webber & Ball (1980) provided evidence of introgressive hybridization which is toward *L. europaeus.* They reviewed a number of characteristics which previous authors (Fernald, 1950; Gleason, 1952; Henderson, 1962) used to separate the species. These characteristics include stems, leaves, indumentum, bracteoles, calyx, corolla, anthers, and nutlets. Webber & Ball concluded that the majority of individuals studied from five populations were intermediate between the two species. The intermediates showed no reduction in effective fertility, apparently representing a not-well documented phenomenon of a European wetland species hybridizing with a native North American species, with the resulting fertile hybrids spreading in the lower Great Lakes region and along the St. Lawrence River.

During the summers of 1978 and 1979, we studied characteristics of many natural populations containing individuals of both species and numerous plants with features intermediate between the two species (Fig. 1). At several sites these plants were locally common at the edges of ponds on the islands and along the shore of southwestern Lake Erie (in Erie, Lucas, and Ottawa Counties). The

Fig. 1. Photograph of young plants intermediate between *Lycopus americanus* and *L. europaeus* from Terwilliger's Pond, Ottawa Co., Ohio, taken late June 1979.

principal study sites with mixed populations were at Magee Marsh (in Lucas County) and Terwilliger's Pond on South Bass Island, Haunck's Pond on Middle Bass Island, and East Harbor State Park (all in Ottawa County). Locations of these sites are provided in Stuckey (1968) and Stuckey & Phillips (1970). In addition to an analysis of herbarium specimens, data were obtained from plants grown under greenhouse conditions and from a habitat analysis of one population in the field. Greenhouse studies provided additional evidence for introgressive hybridization, and the field studies revealed that *L. americanus* is somewhat separated from *L. europaeus* and the intermediates on the basis of differences in habitat.

ANALYSIS FROM MATURE DRIED PLANTS

Over 280 mature plants were obtained from natural populations in the three-county area bordering western Lake Erie, in addition to plants of *L. americanus* from pond 1b at the Delaware Wildlife Area, Delaware Co., Ohio, and specimens of both species in the herbarium of The Ohio State University. Plants from the field were pressed, dried, and examined as to root system, branching patterns of stems, leaf dimensions, color and texture of foliage, indumentum, flowers, and shape of nutlets. The most useful characteristics to separate the two species were derived from nutlets and leaves. With respect to the leaves, the most reliable characteristics were the ratio of length to width of upper cauline leaves and the sinus indentation of lowermost cauline leaves. The

positions measured on a leaf are shown in Fig. 2. The distinguishing characteristics for each species are listed in Table 1.

Using the ratio of width to length of apical cauline leaves and percentage of sinus indentation of lower cauline leaves, plants of *L. americanus* from pure populations at Portage River, Ottawa Co., and Irwin Prairie, Lucas Co., were compared with specimens of *L. europaeus* from Europe and elsewhere in North America filed in the herbarium of The Ohio State University. Following Anderson (1949), measurements from 14 plants of each species were plotted on a scatter diagram (Fig. 3). These plants were widely separated on the scatter diagram. To this diagram was added a sample of 38 plants from Terwilliger's

TABLE 1. Distinguishing characteristics of *Lycopus americanus* and *L. europaeus* based on dried, pressed plants from natural populations.

	L. americanus	*L. europaeus*
Leaves		
apical segment	acute to acuminate	acute to obtuse
texture	thin and smooth	thick and somewhat rough
lateral veins	inconspicuous, not easily seen	prominent, easily seen
color	green to pale-green	green to dark-green
indumentum	mostly glabrate	mostly puberulent
length/width ratio of upper cauline leaves (measured at third or fourth node)	usually 6, ranging from 4 to 14	usually 2.5, ranging from 1.5 to 5
lobing of upper cauline leaves	serrate to acute	acute to obtuse
sinus indentation of lower cauline leaves (measured at lowest three nodes)	usually 70% to midrib, ranging from 40 to 97%	usually 40% to midrib, ranging from 10 to 55%
sinus angle	usually acute	usually obtuse
Nutlets		
length/width ratio	twice or more as long as wide	three-fourths as wide as long
collar	open	slightly open or closed forming a ring
Stems		
branching	usually at basal and middle portion of plant	usually at basal portion of plant
indumentum	pilose to pubescent	villous
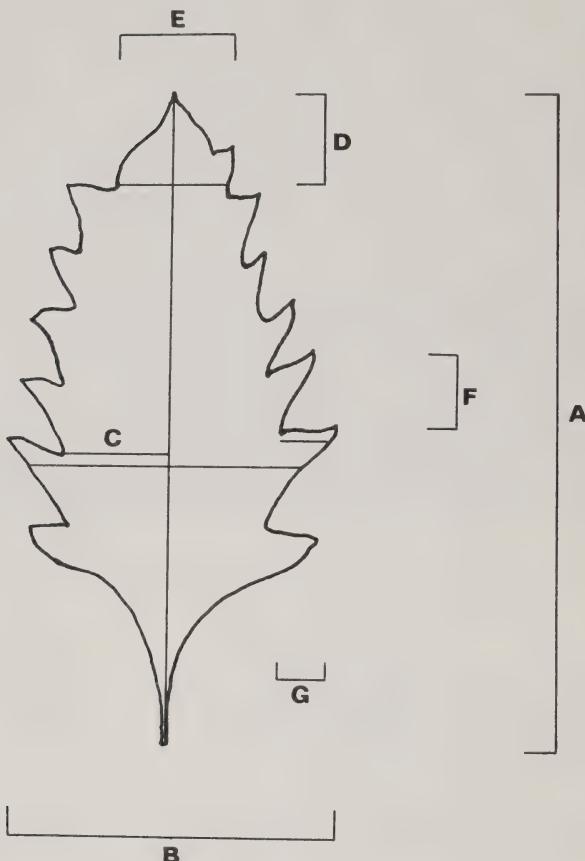
Fig. 2. Diagram of leaf from an intermediate plant showing where measurements were made and the derived calculations, where A = length, B = width at widest part, C = edge of leaf to midrib at second sinus from base, D = length of apical segment, E = width of apical segment, F = length of second sinus from base, and G = width of second sinus from base. The following calculations were made:

Ratio of length/width, $\dfrac{A}{B}$.

Sinus indentation of lower cauline leaves, $C - \dfrac{B}{2} \Big/ \dfrac{B}{2} \times 100$.

Ratio of width to length of apical segment of upper cauline leaf, $\dfrac{E}{D}$.

Sinus indentation ratio, $\dfrac{F}{G}$.

Pond. A large number of plants intermediate between the two species as revealed by their position on the scatter diagram suggests that introgressive hybridization has occurred in the population at this pond.

The morphology of the nutlets of *Lycopus* was well illustrated by Hermann (1936), but his paper did not include *L. europaeus*. Webber & Ball noted differences in size of nutlets and in collar shape and showed the differences diagramatically for the two species. Using leaf morphology as a basis for separation, we took nutlets from plants from Terwilliger's Pond considered to be *L. americanus, L. europaeus,* and intermediates (in September 1978). The ratio of width to length was calculated for 258 nutlets. The ratios for each species were determined to be significantly different. However, the ratio of the intermediates was significantly different from *L. americanus,* but not from *L. europaeus* (Table 2). These data suggest that the introgressive hybridization is toward *L. europaeus.* The intermediates exhibited a wide range of variation in nutlet morphology on any given plant, including some nutlets that were similar in size and shape to those of both species.

ANALYSIS OF GREENHOUSE PLANTS

In September 1978, seeds of *L. europaeus* and presumed intermediates were obtained from 20 plants at Terwilliger's Pond. In order to have plants not contaminated by *L. europaeus,* seeds were obtained from 12 plants at pond 1b at the Delaware Wildlife Area (Delaware Co.), 85 miles inland from Lake Erie.
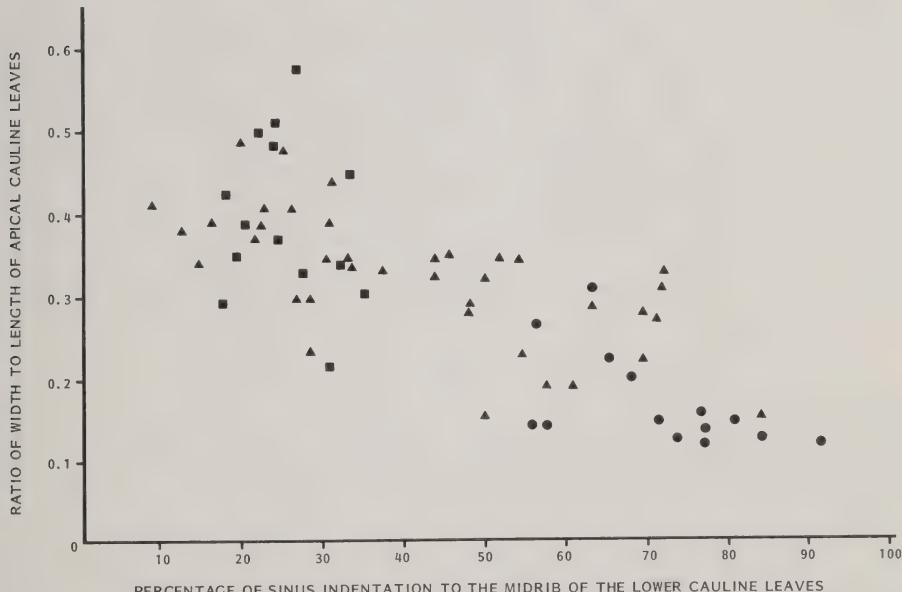

Fig. 3. Scatter diagram of 14 plants of *L. americanus* (dots), 14 plants of *L. europaeus* (squares), and 38 plants from the population at Terwilliger's Pond (triangles).

TABLE 2. Ratios of width to length of nutlets calculated from plants at Terwilliger's Pond.

	Number	Mean ratio of width to length	Range low	high	Standard Deviation
L. americanus	87	0.75	0.51	1.00	0.114
Intermediates	84	0.76	0.56	0.96	0.108
L. europaeus	87	0.77	0.54	0.96	0.075

Based upon two tailed t-test for comparison (Freund, 1973), a significant difference between *L. americanus* and *L. europaeus* was determined at probability 0.01. No significant difference was determined at a probability of 0.01 and 0.05 between *L. europaeus* and the intermediates.

During the subsequent fall and winter, at Baldwin-Wallace College, the seeds were stratified, germinated under growth chamber conditions, and one month later moved to the greenhouse. Measurements were made of stem, leaf, and indumentum characteristics.

Requirements for germination of *Lycopus* seeds are not well known, although Thompson (1969) showed that germination of *L. europaeus* seeds depends on exposure to light and fluctuating temperatures. In the growth chamber, when seeds were subjected to a diurnal fluctuation in temperature and light, considerable difficulty was experienced in germinating *L. europaeus* seeds, with the best germination at ca. 60%. *Lycopus americanus* seeds, under a single fluctuation of temperature and light, had a high germination of more than 80%. The germination of seeds from intermediate plants was low, with a value of less than 20% when subjected to a single or diurnal fluctuation. The morphology of seedlings from intermediate plants was dictated by the temperature fluctuation to which they were exposed. That is, those seeds which germinated under a single fluctuation were close in characteristics to *L. americanus*, and those which germinated under a diurnal fluctuation were either intermediate or close in characteristics to *L. europaeus*. The low percentage of germination of seeds from intermediate plants might be explained in terms of the complex germination mechanisms of *L. europaeus*, as described by Thompson (1969). Because both morphological types appeared in these seedlings, the low percentage of germination is a possible indicator that the seeds were of hybrid origin.

Differences were noted in internode length, leaf shape, and indumentum of the stem and leaves on plants grown under uniform conditions of moisture, temperature, pH, and soil. These features were measured on all the plants within 24 hours approximately three months after germination. Plants of *L. americanus* exhibited uniformly short internodal lengths throughout the plant, whereas plants of *L. europaeus* and plants intermediate between the two species exhibited long internodal lengths from the basal to the middle portion of the plant. Above the middle portion, internodal lengths became shorter (Fig. 4). In total height, plants of *L. europaeus* and the intermediates were more than twice as tall as those of *L. americanus*.

With reference to indumentum, *L. americanus* had shorter hairs on the upper surface of the lower cauline leaves and fewer hairs per unit area on the
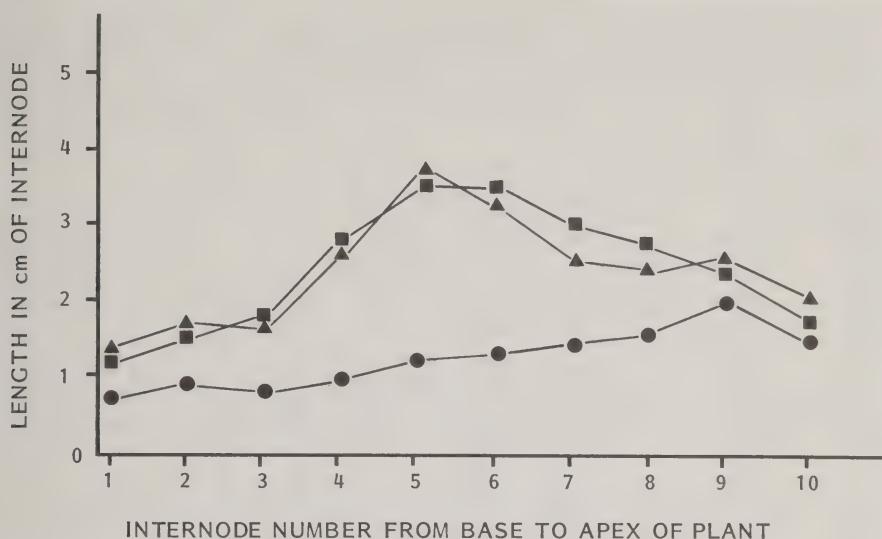
Fig. 4. Average internodal lengths of 47 plants measured after three months in the green-house. *L. americanus* (19 plants, dots), *L. europaeus* (20 plants, squares), intermediates (18 plants, triangles).

stem than did *L. europaeus.* The apical segment of the upper cauline leaves (measured at the third or fourth node from the stem apex) of *L. americanus* had a high ratio (higher than 0.8) of width to length, indicating an acute shape, whereas the apical segment of the upper cauline leaves of *L. europaeus* had a low ratio (lower than 0.5), indicating an obtuse apex. The sinus indentation ratio, determined by measurements at the second sinus from the base on the leaf at the second node from the base of the plant, was larger than 2.2 (deep sinus) in *L. americanus* and smaller than 2.2 (shallow sinus) in *L. europaeus.* These four characteristics are depicted on a scatter diagram (Fig. 5). As shown there, plants considered intermediate between the two species were also inter-mediate in indumentum and leaf characteristics.

EVIDENCE FOR HABITAT SEPARATION

The population at Terwilliger's Pond was studied in late June and through-out July 1979 to determine whether the species could be separated by habitat differences. Twenty-three transects were laid perpendicular to the southeastern shoreline. Each transect, spaced at approximately five meters, included three quadrats one meter apart. Each quadrat was one-fourth square meter (one-half meter on each side). In each transect, one quadrat was next to the water in the wettest soil (low), the second was in a medium-wet soil (medial), and the third was in drier (but still wet) soil higher up the bank of the pond (high). The varia-tion in elevation from the low to the high quadrats was about one-half meter at the maximum. Plants of both species and intermediates were counted in each
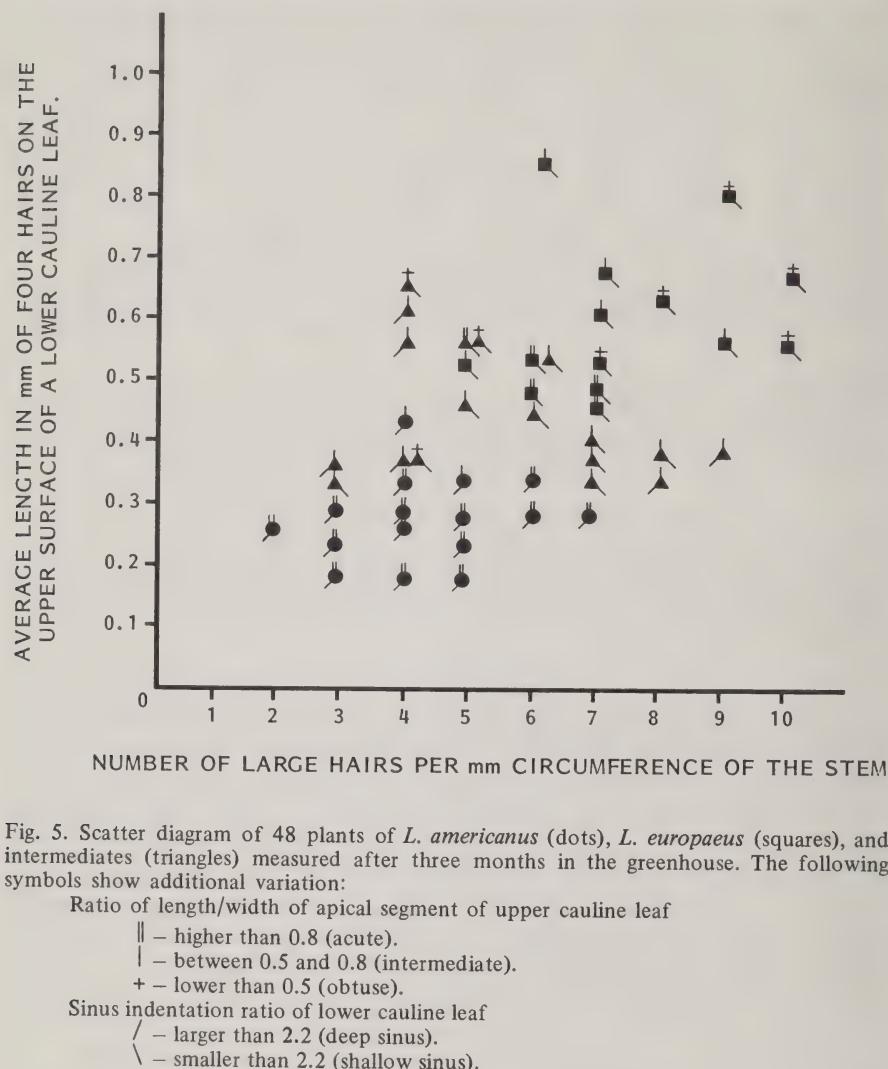
Fig. 5. Scatter diagram of 48 plants of *L. americanus* (dots), *L. europaeus* (squares), and intermediates (triangles) measured after three months in the greenhouse. The following symbols show additional variation:

Ratio of length/width of apical segment of upper cauline leaf
‖ – higher than 0.8 (acute).
| – between 0.5 and 0.8 (intermediate).
+ – lower than 0.5 (obtuse).
Sinus indentation ratio of lower cauline leaf
/ – larger than 2.2 (deep sinus).
\ – smaller than 2.2 (shallow sinus).

quadrat. The frequency of each species and of the intermediates was calculated for all of the low, medial, and high quadrats (Table 3) by dividing the number of plants of a species in 23 similar quadrats by the total number of plants of that species from all 69 quadrats. The distribution of the two species and intermediates appeared to be somewhat related to moisture in the substrate. Of all the plants of *L. americanus*, 42% were in high quadrats, whereas of all the plants of *L. europaeus*, 70% were in low quadrats; of all the intermediates, 42% were in medial quadrats. Thus, plants of *L. americanus* generally grew in drier soil, and those of *L. europaeus* generally grew in wetter soil. At Haunck's Pond,

TABLE 3. Frequency of *L. americanus, L. europaeus,* and intermediates in 69 quadrats (23 low, 23 medial, and 23 high). The actual numbers of plants of each entity occurring in low, medial, and high quadrats was not retained; however, ca. 200 plants were counted in low quadrats, 200 in medial quadrats, and 100 in high quadrats.

Entity	Low	Medial	High
L. americanus	24%	34%	42%
Intermediates	38%	42%	20%
L. europaeus	70%	16%	14%

Magee Marsh, and East Harbor State Park, it was also noted that *L. americanus* generally grew in drier sites, whereas *L. europaeus* and the intermediates occurred closer to the water's edge.

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REVIEW

FERNS OF MINNESOTA. Second Edition, by Rolla Tryon. 165 pp. Univ. of Minnesota Press, Minneapolis, 55414. 1980. ($15.00 cloth, $6.95 paper).

This book provides keys, illustrations, maps, ecological notes, and identification hints for all the ferns and fern allies in Minnesota. It is a second edition of a 1954 work and has been given an extensive "facelift." The text has been re-set in new, more pleasing type, and all the distribution maps have been re-done. Only the illustrations are the same. Lengthy lists of figures and maps have been deleted, maps for a number of hybrid taxa eliminated, and maps for minor varieties consolidated into ones for the species only. The number of maps has been reduced from 85 to 78. The book has been updated in a number of ways. The reference list in the introduction has been modernized, and the distribution maps incorporate the increased knowledge of the 26 years between this edition and the first. Eight pages of color photographs are a particularly welcome addition. *Equisetum kansanum* has been included under *E. laevigatum.* Four additional species are treated: *Polystichum acrostichoides, P. braunii, Asplenium platyneuron,* and *Lycopodium dendroideum.* Not all the additions have been fully incorporated into the text. *Polystichum acrostichoides* and *Asplenium platyneuron* are not keyed, illustrated, or mapped. (The introduction states that there have been three additions, the two *Polystichum* spp. and *Asplenium platyneuron,* and implies that none are incorporated into the text.)

The claim that this edition "contains the changes in nomenclature and classification that are needed to reflect our modern knowledge of the plants" is somewhat misleading. Save for the deletion of some varietal taxa, one has to search diligently for any changes in nomenclature and classification. In fact, the nomenclature and classification are essentially identical to that in the first edition. It is dismaying to see no mention of names like *Dryopteris expansa* or *Lycopodium digitatum,* now becoming widespread in fern literature. Also, the fern families recognized in this edition are identical to those in the first edition. The keys are identical except for those to *Equisetum* and *Lycopodium,* and the text under each species is essentially unchanged. The great amount of information (especially about complex genera such as *Dryopteris* or *Botrychium*) that has come to light since 1954 is not considered. It is stated that inclusion of this material would have required more space and make the treatment more technical. However, it should have been possible to update the taxonomy without detailed treatments of underlying arguments or at least to note that there have been new interpretations. Surely taxonomists do not refuse to accept new concepts simply because their exposition takes a few more lines of print. In short, if you are looking for a completely up-to-date treatment, you will be disappointed. This is unfortunate since fern enthusiasts are invariably keen to know about recent developments in the understanding of their favorite plants.

The small changes made in the text have occasionally left their mark in mixups in maps and legends. For example, Map 32, said to be *Dryopteris fragrans* var. *remotiuscula* in the legend (but not in the text), is actually *Polystichum braunii.*

The book does fulfill its stated purpose of being a manual for the identification of the kinds of ferns in Minnesota and supplying information on habitats and distributions. Although not as up to date as many might wish, it is useful for most ferns, and the updated distribution maps are most welcome. It is a worthwhile addition to one's fern library.

—A. A. Reznicek

245 THE HAMPTON CREEK WETLAND COMPLEX
IN SOUTHWESTERN MICHIGAN
I. HISTORY AND PHYSICAL FEATURES

Kenneth J. Sytsma[1] and Richard W. Pippen

Dept. of Biology
Western Michigan University
Kalamazoo, 49008

Wetlands have sometimes been considered lacking in natural or economic values. Small lakes, ponds, swamps, meadows, fens, and bogs have been drained, filled, and subjected to other abuses in order to provide space for farmland, highway construction, waste disposal, and development of private, commercial, and industrial complexes. It is estimated that over one-third of the original wetland acreage in the United States has disappeared (Shaw & Fredine, 1956). Though Michigan has a high acreage of wetland, as do most of the glaciated northern states, the average size of individual wetlands is small (Wetzel, 1975). These wetlands, therefore, are particularly susceptible to the pressures of human impact.

The natural values of wetlands—production of wildlife habitats, buffering flood waters, recharging groundwater, trapping manmade pollutants, and development of recreational sites—have largely been ignored. The importance of wetlands is most obvious when floristics is examined. Almost 40% of the threatened, endangered, and probably extinct plant species in Michigan are found in aquatic or wetland habitats (Beaman, 1977). The few floristic studies done on specific sites in Michigan indicate that wetlands maintain a unique assemblage of rare or threatened plants (Brewer, 1965; Cain & Slater, 1948; Crow, 1969; Gates, 1942; Hayes, 1964; Keough & Pippen, 1981; Thompson, 1968).

Only in the last few years has concerted action been taken to protect wetlands with their unique flora and associated fauna. Legislation has been passed to initiate wetland inventories at the federal level by the U. S. Fish and Wildlife Service (Golet & Larson, 1974) and the state level by the Michigan Dept. of Natural Resources. However, the immense size of the area covered by these inventories prevents in-depth studies of most wetland sites. The information presented in this series of papers on the vegetation, ecology, and succession of a wetland complex in southwestern Michigan is the result of an in-depth, three year study and has as one of its primary aims the protection and preservation of an unique assemblage of rare and threatened plants (Table 1).

The 24 ha (60 acre) Hampton Creek wetland complex is located in the northern part of the Gourdneck State Game Area, Portage Township, Kalamazoo Co. (T3S, R11W, NW 1/4 of Sect. 19), 150 m southeast of the intersection of US 131 and Centre Street. According to the original land survey, this portion of the county was dominated by oak-hickory forest with large beech-maple forest and prairie sites to the south and southwest (Kenoyer, 1930). The entire study area is owned and managed by the Michigan Dept. of Natural Resources. It is located at 260 to 265 m above sea level on sandy, glacial stream beds and out-

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[1] Present address: Dept. of Biology, Washington Univ., St. Louis, MO, 63130.

TABLE 1. Rare and threatened species in the Hampton Creek wetland complex and surrounding communities.

	Community	Abundance[1]	Status[2]
Amorpha canescens	Dry Prairie	Few	Rare
Asclepias amplexicaulis	Dry Prairie	Scattered	Rare
Berula pusilla	Emergent Aquatic	Abundant	Threatened
Calamagrostis stricta	Wet Fen	Scattered	Threatened
Chimaphila maculata	Pine Forest	Few	Rare
Coreopsis palmata	Dry Prairie	Scattered	Threatened
Cypripedium calceolus var. parviflorum	Wet Fen	Few	Rare
C. candidum	Wet Fen	Scattered	Threatened[3]
Eryngium yuccifolium	Wet-Mesic Prairie	Few	Threatened
Habenaria ciliaris	Wet-Mesic Prairie	Few	Threatened
Lygodium palmatum	Shrub-Carr	Few	Threatened
Silphium integrifolium	Mesic Fen	Abundant	Threatened
Smilax herbacea	Hardwood Forest	Scattered	Rare
Swertia caroliniensis	Dry Prairie	Scattered	Rare

[1]Few—less than 10 individuals in the study area; scattered—10 or more individuals but grouped in widely spaced populations; abundant—numerous individuals usually in large populations.
[2]Based on Wagner et al., 1977.
[3]Threatened throughout its range in the U. S. (Ayensu & DeFilipps, 1978).

wash derived from the Kalamazoo lateral moraine of Wisconsinan age farther west in Texas and Oshtemo Townships. Approximately 98 m of porous glacial sand and gravel cover the pre-Pleistocene bedrock of calcareous Coldwater Shale (Straw, 1978). Calcium bicarbonate-rich groundwater enters the area from springs at several points throughout the site. These points are quite conspicuous during mild weather in winter since they do not freeze over as do adjacent areas. Extensive layers of alkaline sedge and woody peat have formed over most of the area to depths of as much as 3.5 m. Drainage occurs laterally through or over the peat and empties into Hampton Creek, a meandering stream that has a constant source of water from springs 0.5 km west of the study area. This wetland watershed with its groundwater springs is important in terms of water supply for Kalamazoo County; three to five million gallons of water per day pass through this system before emptying into Hampton Lake (based on mid-summer low flow data from the Alamo-Oshtemo Groundwater Reservoir Water Supply Paper, Plate 4, 1973).

The study area was restricted to land owned by the Dept. of Natural Resources and therefore did not include the peatland and lowland forest adjacent to Hampton Lake on the eastern border of the study area. This forest is dominated by *Acer rubrum* (Red Maple), *Alnus rugosa* (Speckled Alder), *Fraxinus nigra* (Black Ash), *Prunus serotina* (Wild Black Cherry), and *Ulmus rubra* (Slippery Elm) but interspersed with peatland areas. Angling Road, which runs parallel with US 131, marks the western border of the study area. The northern border is composed of a ridge of oak forest dominated by *Quercus alba* (White Oak), *Q. borealis* var. *maxima* (Red Oak), and *Q. velutina* (Black

Oak); a small reforestation area of *Pinus resinosa* (Red Pine); and several dry, sandy, prairie areas. The ridge, 6 m above the study area at its greatest elevation, slopes directly down to the creek. In 1958 the Consumers Power Company cleared a 30 m-wide powerline right-of-way at the edge of the oak forest and a wet-mesic prairie site located in the study area. The southern border is composed of Red Pine, Jack Pine (*Pinus banksiana*), and Scotch Pine (*P. sylvestris*) plantations; an oak forest; and a large, dry, sandy area. The dry prairie sites, also owned by the Dept. of Natural Resources, contain an assemblage of rare and threatened plants, including *Amorpha canescens* (Lead-plant), *Asclepias amplexicaulis* (Clasping-leaved Milkweed), *Chimaphila maculata* (Spotted Wintergreen), *Coreopsis palmata* (Prairie Tickseed), *Quercus prinoides* (Dwarf Chinquapin Oak), and *Swertia caroliniensis* (American Columbo). The general aspect of the study area can be seen in Fig. 1.

The study area has had some disturbance. Most of the area was purchased around 1920 by a family of Italian immigrants who attempted to cultivate onions or celery in the rich organic peat (pers. comm., Charles Cook, a local resident). They dug ditches from the springs to the creek in order to drain the land. These ditches are still present in several of the peat areas. Efforts at farming were not successful, and in 1940 the land was sold to the Dept. of Natural Resources (then called the Dept. of Conservation). The Department farmed the dry areas for 20 years with corn, alfalfa, clover, and bushclover. In 1948 and 1949, with the help of local college students, the Department planted Jack and

Fig. 1. Oblique aerial photo of the central portion of the Hampton Creek wetland complex taken from the south end on November 10, 1978. Hampton Creek appears gray due to the thick mat of *Nasturtium* and *Veronica*. The light-colored trees are *Larix laricina* (Tamarack) shedding their yellow needles. The Consumers Power Co. right-of-way is seen at the north edge of the complex.

Red Pine on the dry north and south borders of the wetlands and Flowering Dogwood, Nannyberry, and Multiflora Rose in wetter sites. Parts of Hampton Creek were straightened two or three times when US 131 was under construction in the early 1960's. The creek was once a habitat for trout, and the banks provided nesting for woodcocks, but suitable conditions were destroyed by the straightening process (pers. comm., Charles Cook). No record or evidence of fire in the study area was found.

The climate of the Gourdneck State Game Area is modified by Lake Michigan, about 40 miles to the west, because of the prevailing westerly winds. The surface temperatures of Lake Michigan average higher than the land temperatures from September to March and lower from April to August. This temperature lag produces a number of climatic changes referred to as "lake effects" that are usually noticed up to 40 miles inland (Eichenlaub, 1978). Summer winds moving across Lake Michigan are cooled, whereas winter winds are warmed. This phenomenon produces cooler but drier summers and warmer but wetter winters than those found on the western side of Lake Michigan.

Weather data from the Kalamazoo State Hospital Weather Station six miles north of the area show that the mean high temperature for 1914-70 was 35°C (96°F) and the mean low temperature was -22°C (-7°F). The mean annual temperature for the same period was 10°C (49.3°F). The mean growing season is 153 days, from May 9 to October 9, the average last spring date and first fall date with freezing temperatures.

In summer the cooler water of Lake Michigan reduces cloud cover 15% and precipitation 10% from the expected values, and in winter the warmer lake water increases cloud cover 35% and precipitation 25% (Eichenlaub, 1978). Precipitation averages 85 cm (34.71 in.) per year, with May and June the peak months. The average precipitation ranges from a high of 9 cm (3.81 in.) in June to a low of 4.8 cm (1.99 in.) in February. Snowfall averages 170.8 cm (69.7 in.) but was considerably higher during the period when the study was performed; for 1977 and 1978 it was 172.7 cm (70.5 in.) and 210.7 cm (86 in.), respectively (USDC, 1977, 1978).

Soil samples from the first 8 cm below the litter layer were obtained on October 31, 1978 from all the community types in the heterogeneous wetland complex. (The classification of community types will be presented in the second paper of this series.) The samples were oven-dried at 38°C (100°F) for two days and then screened through a 2 mm wire mesh to remove plant fibers and fragments. The dried samples were tested for content of calcium, magnesium, ferric iron, sulfate, nitrate nitrogen, nitrite nitrogen, and ammonium nitrogen, as well as pH, with a LaMotte Soil Testing Outfit (Model STH-14). Water samples were collected from Hampton Creek and the spring sites periodically during the 1978 growing season and once during winter. A Hach Portable Water Kit (Model AC-DR-EL) was used to obtain pH, alkalinity, total hardness, and dissolved O_2.

This wetland complex has a diverse array of soil types (Table 2). Wet and moderately decomposed sedge and graminoid peat composes the bulk of peat underlying the sedge meadow, fen, *Cornus* shrub-carr, *Betula-Potentilla* shrub-carr, and wet northern forest communities. Occasional layers of woody shrub remains are found at different depths in the peat beneath the fen, shrub-carr, and forest sites. The uppermost (0.5 m) peat layers in the fen sites are some-

TABLE 2. Soil characters of plant communities[1] in the Hampton Creek wetland.

	pH	Calcium ppm	Magnesium ppm	Ferric ppm	Sulfate ppm	Nitrate ppm	Nitrite ppm	Ammonium ppm
Emergent Aquatic								
Nasturtium-Veronica	6.5	12,000	16	2	20	5	0	0
Typha-Iris	5.6	3,500	4	50	0	0	1	5
Typha-Scirous	6.5	14,000	20	0	0	5	0	5
Southern Sedge Meadow	5.4	700	8	30	0	0	3	5
Fen	6.4	12,000	40	0	0	5	0	5
Wet-Mesic Prairie	5.1	375	4	15	0	0	0	0
Southern Shrub-Carr								
Cornus	6.3	7,000	20	0	0	5	0	0
Betula-Potentilla	8.3	10,000	12	0	0	5	0	0
Toxicodendron-Osmunda	5.0	0	4	5	0	0	0	0
Wet Northern Forest	4.4-6.4	9,500	22	2	0	5	0	0
Wet-Mesic Southern								
Hardwoods	5.3	700	8	2	0	5	0	0

[1]Community types are described in the second paper of this study.

what decomposed or mineralized, and in the forest sites are composed of woody peat only or with a slight accumulation of *Sphagnum* peat. The emergent aquatic sites associated with the groundwater springs have a soil profile considerably different from that of the other sites. Almost 2 m of mixed sand and marl sediments cover the glacial sand with a layer of finely decomposed, black, aquatic peat or muck on top. Sedge and graminoid peat has accumulated to 0.5 m in the hummock areas surrounding the groundwater springs.

Most of these communities have circumneutral pH values, although the wet northern forests that have accumulated *Sphagnum* peat have lower pH values. The surface peats in all these sites show high amounts of calcium, ranging from 9,000 ppm to a high of 14,000 ppm in the emergent aquatic community (Table 2). Magnesium is the only other major nutrient present in considerable amounts.

Sandy soils, that are prevalent in the dry areas adjacent to the wetland complex, are significant in the wet-mesic prairie, *Rhus-Osmunda* shrub-carr, wet-mesic southern hardwoods, and *Nasturtium-Veronica* emergent aquatic communities. Except for the *Nasturtium-Veronica* community, these communities also have acidic soil with very little calcium and magnesium.

The largest water sources for the wetland complex are the groundwater springs located in fen sites and in the area west of the study site that supplies the water for Hampton Creek. Periodic water samples taken from the fen sites and from both the inlet and outlet of Hampton Creek indicate an average alkalinity of 220 mg/1 $CaCO_3$, total hardness of 240 mg/1, pH of 6.6, and dissolved O_2 at 82% of saturation. These values fluctuated very little from season to season, and values from all sites at one given time were similar. The hardness of these groundwater sources is instrumental in the formation of calcareous conditions prevalent in most of the complex.

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GRIMMIA TENERRIMA, A MOSS NEW TO MICHIGAN

Allan J. Fife

Dept. of Botany and Herbarium
University of Michigan
Ann Arbor, 48109

A recent collection of *Grimmia tenerrima* Ren. & Card. from Isle Royale provides the first record of this species from Michigan and the Great Lakes region. This species is widely distributed in montane regions of western North America but is known in eastern North America from only a scattered few localities. The Isle Royale collection came from a granite ledge at the shore of Lake Superior at Tobin Harbour, Keweenaw Co. (*Fife 3160;* MICH; also *in herb.* Fife).

Material in the University of Michigan herbarium has been studied and North American specimens have been confirmed from California, Colorado, Idaho, Montana, Washington, Wyoming, Alberta, and British Columbia. In the West, *Grimmia tenerrima* is restricted to alpine situations (apparently most often on granite, occasionally on mafic rocks) and occurs at higher elevations in the

southern portion of its range. The Michigan collection is from a non-alpine locality, but the microclimate of exposed shorelines of the northern Great Lakes is severe, and a variety of predominantly alpine and arctic plants are known to occur in such situations. A collection from an alpine plateau of about 1300 ft. elevation in Newfoundland was the only eastern North American specimen readily available for confirmation. *Grimmia tenerrima* has been reported from Greenland and the Gaspé (Jones, 1933, as *G. alpestris*) and the White Mountains of New Hampshire (Crum & Anderson, 1981). Brassard & Weber (1978) reported *G. tenerrima* from Labrador, but a duplicate of one of the two collections they cited is misdetermined. The species has been reported from Iceland, northern, western, and central Europe, Corsica, Sardinia, Altai, and Kashmir.

Grimmia tenerrima may be added to a sizable list of mosses having the major portion of their North American distribution in the West, with scattered populations also in the upper Great Lakes and the Gulf of St. Lawrence regions. This distribution pattern was first discussed by Steere (1937), who considered the possibility of nunatak survival during glacial periods.

The sexuality of *Grimmia tenerrima* varies. In western North America the species is generally dioicous, but autoicous forms have been described and given varietal rank (Jones, 1933). The Michigan collection appears to be dioicous. Material from Newfoundland (*Fife 2186*, MICH, NFLD), however, is autoicous; Smith (1978) reported that *G. tenerrima* (cited as *G. alpestris*) is autoicous in Britain.

The taxonomic status of *Grimmia tenerrima* remains controversial, with the most persistent problem centering on its relationship with *G. montana* BSG, another species occupying montane habitats in western North America. Most recent authors separate these species using the unsatisfying characters of vegetative leaf length, the fraction of the length of the leaf which is bistratose, and the relative development of an opercular rostrum. Additionally, these two species are reported to be restricted to different elevational ranges in the West. Some western North American material is difficult to name satisfactorily using these criteria. However, the Michigan material reported here clearly belongs to what is presently accepted as *G. tenerrima*. *Grimmia montana* is not known to occur in eastern North America, and the eventual resolution of this taxonomic problem will not diminish the phytogeographical significance of the Michigan collection.

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The March issue (Vol. 20, no. 2) was mailed April 23, 1981.

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On the cover: Trillium grandiflorum
at Baker Woodlot on the campus
at East Lansing; photo by Hannah Priwer

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THE HAMPTON CREEK WETLAND COMPLEX IN SOUTHWESTERN MICHIGAN.
II. Community Classification

Kenneth J. Sytsma[1] and Richard W. Pippen

Dept. of Biology
Western Michigan University
Kalamazoo, 49008

Communication about wetland vegetation is difficult because of the wide variation in wetland types, the diverse backgrounds of those interested in wetlands, and the multiplicity of terms and concepts, many of which are defined according to the discipline of the user (Jeglum et al., 1974). This problem of wetland terminology applies in Michigan due to the presence of several different, well-marked floristic regions. Since the majority of wetland studies in Michigan have been confined to the northern Lower Peninsula and the eastern Upper Peninsula, this problem is compounded. The scarcity of wetland information in southern Michigan leads to the use of terminology and concepts obtained from studies in other floristic regions in Michigan—a potentially misleading practice. The information presented here on the community classification of the Hampton Creek wetland complex in southwestern Michigan (previously described by Sytsma & Pippen, 1981) should be of interest because of the lack of these studies in this area, the extreme heterogeneity giving rise to numerous wetland types and a number of rare or threatened plants associated with the wetland types.

The study was done from 1977 to 1979. The study area was visited two or three times a week throughout the growing season and periodically during the winter. Aerial photo enlargements were initially used to identify the major plant community types. Due to the large size of the area and the extreme heterogeneity or patchiness of many of the communities, quadrat or transect sampling of all the major types was impractical, and so the relevé method (Mueller-Dombois & Ellenberg, 1974) was used. Vegetation characteristics of each community type were obtained by determining species presence in a number of small patches representative of the larger community type. Due to the floristic similarities of southern Wisconsin and southwestern Michigan, the community classification as given by Curtis (1959) was used to identify the major wetland types. Where applicable, subtypes were also differentiated and named by the dominant genus or genera in the subtype.

Floristic similarity (Fig. 2) was determined for each pair of communities using a measure based on species presence (Greig-Smith, 1964). In two communities, one with a number of species and another with b number of species, and c species occurring in both communities, similarity is indicated as follows:

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[1] Present address: Dept. of Biology, Washington University, St. Louis, MO, 63130.

$$\text{Index of similarity} = \frac{2c}{a+b}.$$

The index ranges from 0 to 1.0 and expresses the range from no similarity to complete similarity, respectively.

The wetland complex is unique because of the diversity and juxtaposition of plant communities. The vegetation consists of seven major communities: emergent aquatic, southern sedge meadow, fen, wet-mesic prairie, shrub-carr, wet northern forest, and wet-mesic southern hardwoods. The emergent aquatic community can be differentiated into three subtypes: *Nasturtium-Veronica, Typha-Iris,* and *Typha-Scirpus.* Shrub-carr can also be differentiated into three subtypes: *Cornus, Betula-Potentilla,* and *Toxicodendron-Osmunda.* The lack of floristic similarity within the emergent aquatic and shrub-carr communities necessitated the formation of these subtypes. Community types are mapped in Fig. 1. (Owing to small scale, the map portrays the basic pattern but not the patchiness of heterogeneity of many of the communities.)
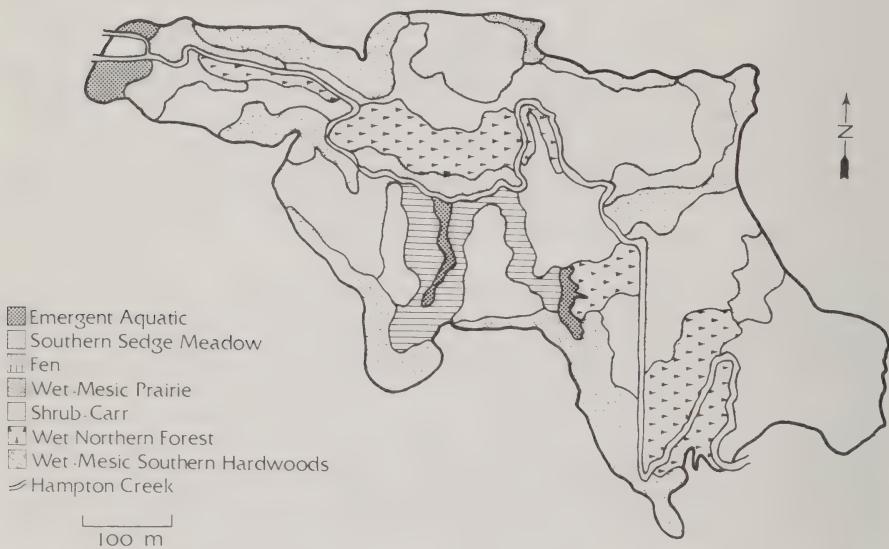
Fig. 1. Map of plant communities in the Hampton Creek wetland complex (adapted from an enlarged aerial photograph).

Emergent Aquatic Community

The emergent aquatic community, or marsh, exists in those areas where water is above the soil most of the year. Three subtypes of the community can be differentiated. The *Nasturtium-Veronica* subtype is found only in Hampton

Creek and the small channels draining the fen communities. *Nasturtium officinalis* (Watercress) and *Veronica catenata* (Water Speedwell) are the dominant members of this community. They form an almost complete mat over the stream by late September. By early November, the stream with its solid green mat of *Nasturtium* and *Veronica* provides a sharp contrast to adjacent wetlands with brown, senescing vegetation. These mats can form extensive, permanent communities in the bends of the meandering stream. Important members of these mat communities are *Aster lucidulus* (Glossy-leaved Aster), *Berula pusilla* (Cut-leaved Water Parsnip), *Bidens cernua* (Nodding Bur Marigold), *Carex stricta* (Sedge), *Cicuta bulbifera* (Bulblet Water Hemlock), *Eleocharis smallii* (Spike-

EA1										
.04	EA2									
.15	.29	EA3								
.18	.09	.25	SM							
.19	.12	.53	.52	FN						
0	0	.05	.12	.11	WMP					
.03	.06	.08	.13	.10	.08	SC1				
.04	.15	.14	.10	.10	0	.10	SC2			
0	0	.03	.11	.07	0	.04	.05	SC3		
.07	.11	.26	.30	.32	.05	.19	.17	.09	WF	
0	.03	.05	.13	.09	.02	.20	0	.17	.19	WMH

Fig. 2. Index of similarity for each pair of communities in the Hampton Creek wetland complex. Community types and subtypes are abbreviated: Emergent aquatic *(Nasturtium-Veronica*—EA1; *Typha-Iris*—EA2; *Typha-Scirpus*—EA3), southern sedge meadow—SM, fen—FN, wet-mesic prairie—WMP, shrub-carr *(Cornus*—SC1; *Betula-Potentilla*—SC2, *Toxicodendron-Osmunda*—SC3), wet northern forest—WF, wet-mesic southern hardwoods—WMH.

rush), *Juncus nodosus* (Rush), *Sparganium americanum* (Bur-reed), and *Viola cucullata* (Marsh Violet). The *Nasturtium-Veronica* community is floristically most similar to fen, sedge meadow, and *Typha-Scirpus* communities (Fig. 2).

The presence and abundance of *Berula pusilla* in this community is noteworthy since the Cut-leaved Water Parsnip is threatened in Michigan (Wagner et al., 1977). This western species has been collected in only three other Michigan counties: Cass, Kent, and St. Joseph. It has its greatest abundance in channels draining groundwater spring sites.

The *Typha-Iris* subtype is found in depressions commonly associated with wet sedge meadows. The cat-tail marsh is usually more temporary than the other two emergent aquatic communities since it does not have a constant water source but derives most of its water from run-off or precipitation. *Typha latifolia* (Cat-tail) and *Iris virginica* (Blue Flag) are the prevalent members in the community. The sedge *Carex aquatilis, Eleocharis erythropoda* (Spike-rush), *Lemna minor* (Lesser Duckweed), *Lycopus americanus* (Water Horehound), and *Thelypteris palustris* (Marsh Fern) are also significant components in these depressions. This community is floristically most related to the *Typha-Scirpus* emergent aquatic community (Fig. 2).

The *Typha-Scirpus* marsh associated with the sites of groundwater springs is dominated by *Scirpus acutus* (Hardstem Bulrush), *Thelypteris palustris,* and *Typha latifolia.* The groundwater is extremely calcareous and has a major impact on the species composition of these sites. Species characteristic of very hard water are *Agalinis purpurea* (Purple Gerardia), *Campanula aparinoides* (Blue Marsh Bellflower), *Drosera rotundifolia* (Round-leaved Sundew), *Lobelia kalmii* (Brook Lobelia), *Oxypolis rigidior* (Cowbane), *Tofieldia glutinosa* (False Asphodel), *Triglochin palustre* (Marsh Arrow Grass), and *Utricularia intermedia* (Flat-leaved Bladderwort). The macro-alga, *Chara* (Stonewort), is abundant in these groundwater seepage sites and contributes to the production of a marly, aquatic peat. *Carex stricta* forms raised mounds of sedge peat above water level. These spring sites, therefore, are composed of a series of quaking, interconnected hummocks with adjacent soft-bottomed pools. Fen communities usually border these springs sites, and it is not surprising, therefore, that these two communities have the greatest floristic similarity of any community pair in the complex (Fig. 2).

Southern Sedge Meadow

The southern sedge meadow is an open community where sedges rather than grasses contribute more than half the dominance. The dominance of *Carex* species rather than *Scirpus* species separates southern sedge meadows from northern meadows. The muck or raw peat soil is typically flooded in the spring but lies just above the water table for most of the growing season. However, extreme variation in the moisture content is found in the sedge meadows, which correlates with species composition. *Carex stricta* is the most prevalent sedge and forms extensive "tussock meadows" (Stout, 1914). In the wetter sedge meadows, *Carex aquatilis, C. atlantica, C. buxbaumii, C. hystericina, Juncus effusus* (Rush), and *Scirpus cyperinus* (Wool-grass) tend to associate with *Carex*

stricta along with the grasses *Agrostis gigantea* (Redtop), *Bromus ciliatus* (Fringed Brome), *Calamagrostis canadensis* (Blue-joint), and *Glyceria canadensis* (Rattlesnake Grass). The prominent forbs characteristic of these wet sedge meadows include *Aster lucidulus* (Glossy-leaved Aster), *Eupatorium maculatum* (Joe-pye Weed), *E. perfoliatum* (Boneset), *Lathyrus palustris* (Marsh Pea), *Scutellaria galericulata* (Marsh Skullcap), *Solidago rugosa* (Rough-leaved Golden-rod), *Spiraea alba* (Meadowsweet), *S. tomentosa* (Hardhack), and *Thelypteris palustris* (Marsh Fern).

In the drier meadows, including those drained for cultivation in the 1920's, *Carex bebbii* and *C. scoparia* replace the more hydric sedges and codominate with *Carex stricta. Agropyron trachycaulum* (Wheatgrass) and *Poa compressa* (Kentucky Bluegrass) replace the more hydric grasses except for the ubiquitous Blue-joint. A similar replacement of the characteristic hydric forbs is seen by *Cicuta maculata* (Water Hemlock), *Onoclea sensibilis* (Sensitive Fern), *Poly-gonum sagittatum* (Arrow-leaved Tear Thumb), *Rubus hispidus* (Swamp Dew-berry), *Solidago canadensis* (Canada Goldenrod), and *Thalictrum dasycarpum* (Tall Meadow Rue). These dry sedge meadows are also being invaded by *Populus grandidentata* (Large-toothed Aspen) and *P. tremuloides* (Trembling Aspen). This invasion by aspens is not unusual. Catenhusen (1950) has shown that in Wisconsin aspens quickly invade sedge meadows that have been either drained or burned.

Fen

The use of the term "fen" has caused much confusion in wetland ecology. It has been used to describe marsh, sedge meadow, bog, wet prairie, and woody communities. The British ecologist Tansley (1949) defined fen strictly as a com-munity dominated by grasses and forbs rather than sedges and located on an alkaline or neutral peat with a hard groundwater source, the definition Curtis (1959) adopted for the classification of similar communities in Wisconsin. In the northern Great Lakes region the definition of fen has been broadened to include any mineral-rich peatland (Boelter & Verry, 1977; Heinselman, 1970; Jeglum et al., 1974). Using the stricter definition in this study, fen is differentiated from "marsh" with mineral soil, "sedge meadow" with sedges as dominant plants, "bog" with acidic peat, "wet prairie" without an internal supply of bicarbonate-rich water, and "forest" or "swamp" with trees as dominants.

Fen communities are found in two large sites with wet and quaking peat that has formed where calcium and magnesium bicarbonate-rich groundwater seeps to the surface. In the southern Great Lakes region, fen is regarded as a hybrid community composed of selected species from the major formations as they passed through the region after glaciation (Curtis, 1959). This idea is sup-ported by the floristic similarity the fen community has with other wetland communities, especially sedge meadow, *Typha-Scirpus* emergent aquatic, and wet northern forest types (Fig. 2). A western element is well represented in the fen community by *Andropogon gerardii* (Big Bluestem), *Cacalia plantiginea* (Tuberous Indian Plantain), *Eupatorium maculatum* (Joe-pye Weed), *E. perfoliatum* (Boneset), *Gentiana andrewsii* (Closed Gentian), *Hypoxis hirsuta*

(Yellow Star Grass), *Liatris spicata* (Blazing Star), *Silphium integrifolium* (Entire-leaved Rosinweed), *Solidago riddellii* (Prairie Goldenrod), *Sorghastrum nutans* (Indian Grass), *Veronicastrum virginicum* (Culver's-root), and *Zizia aurea* (Golden Alexander).

The northern element is represented by the dominant *Potentilla fruticosa* (Shrubby Cinquefoil) and the characteristic fen species *Aster junciformis* (Bog Aster), *Bromus ciliatus* (Fringed Brome), *Calamagrostis stricta* (Narrow Reed Grass), *Gentiana procera* (Fringed Gentian), *Parnassia glauca* (Grass-of-Parnassus), and *Salix candida* (Sage Willow). The eastern and southeastern element is characterized by *Agalinis purpurea* (Purple Gerardia), *Aster puniceus* (Purple-stemmed Aster), and *Muhlenbergia glomerata* (Marsh Wild-timothy). Other species commonly found in fens include *Carex prairea* (Prairie Sedge), *Castilleja coccinea* (Indian Paintbrush), *Cypripedium calceolus* var. *parviflorum* (Small Yellow Lady's Slipper), *C. candidum* (White Lady's Slipper), *Solidago ohioensis* (Ohio Goldenrod), and *Spiranthes cernua* (Nodding Ladies'-tresses).

Four species of the fen sites are considered rare or threatened in Michigan. *Calamagrostis stricta* (Narrow Reed Grass), typically of boreal habitats, has been collected in only one other Michigan county, Keweenaw, the northernmost Michigan county. The presence of *C. stricta* in these fens, as well as other similar sites in Kalamazoo County, suggests that it has persisted in post-Pleistocene times because of a favorable habitat offered in cold groundwater spring sites. *Cypripedium candidum* (White Lady's Slipper), found in 12 southern counties, is threatened throughout its range in the United States by the destruction of its specialized habitat by man and the rapid rate at which that habitat undergoes succession. Mowing has been shown to aid in the preservation of this species (Curtis, 1946). *Silphium integrifolium* (Entire-leaved Rosinweed) is one of several threatened plants of a "prairie element" that just manages to enter the southwestern counties of Michigan. This tall composite forms large populations in drier fen sites. *Cypripedium calceolus* var. *parviflorum* (Small Yellow Lady's Slipper) is rare in Michigan; its status in the local wet fen sites is precarious— only three plants have been found.

Wet-Mesic Prairie

Wet-mesic prairie is a vegetation community arbitrarily selected from a compositional gradient of prairie communities based on water-holding capacity of the soil (Curtis, 1959). The disturbed wet-mesic prairie site is located on sandy lowlands between a large sedge meadow and a slightly elevated and better-drained mesic-xeric prairie site represented by *Amorpha canescens* (Leadplant), *Andropogon scoparius* (Little Bluestem), *Aster laevis* (Smooth Aster), *Coreopsis palmata* (Prairie Tickseed), *Lithospermum croceum* (Puccoon), and *Solidago nemoralis* (Gray Goldenrod). Due to the porosity of its sandy soil the wet-mesic prairie site is wet on the surface only in spring and is never inundated by standing water, as is the adjacent sedge meadow.

The wet-mesic prairie has been invaded by *Cornus racemosa* (Gray Dogwood) and *Pteridium aquilinum* (Bracken) since being disturbed in 1958 by construction of the powerline. In the few areas not invaded are *Aletris farinosa*

(Colicroot), *Eryngium yuccifolium* (Rattlesnake Master), *Gaultheria procumbens* (Common Wintergreen), *Gentiana andrewsii* (Closed Gentian), *Iris virginica* (Blue Flag), *Rubus hispidus* (Swamp Dewberry), and *Salix humilis* (Prairie Willow). Scattered throughout the site are patches of *Andropogon gerardii* (Big Bluestem) and *Spiranthes cernua* (Nodding Ladies'-tresses). The fact that close to half of these species are also found in fen communities (although not vice versa) emphasizes the floristic similarity of the two communities (Fig. 2).

Eryngium yuccifolium is a threatened plant in Michigan with a range similar to that of *Silphium integrifolium.* Another representative of the "prairie element," *E. yuccifolium,* is found only in Berrien, Cass, Kalamazoo, St. Joseph, and Van Buren Counties. The single population of Rattlesnake Master, as well as the closely associated population of *Aletris farinosa,* did not flower in 1977 or 1978, perhaps due to invasion of *Pteridium aquilinum* that reduced the amount of light reaching the basal rosettes. Removal of the Bracken by selective cutting in the summer of 1978 allowed both Rattlesnake Master and Colicroot to flower in early July 1979. *Habenaria ciliaris* (Orange Fringed Orchid) is also found in the prairie site. This threatened plant is found in 18 counties, mostly southern, but it is not abundant where found. Only five plants have been seen at this site, but they appear to be vigorous. Management of this wet-mesic prairie site is essential for the preservation of these two species.

Southern Shrub-Carr

Southern shrub-carr is a vegetation community occupying wetland sites and dominated by tall shrubs other than alder, which is characteristic of northern shrub-carr. Three subtypes of shrub-carr can be differentiated in the study area. The dominant *Cornus* subtype is composed of extensive clones of *Cornus racemosa* (Gray Dogwood) that occupy 35% of the study area. In drier areas, such as the edges of open sandy areas or prairie sites, chokeberries (*Aronia melanocarpa* and *A. prunifolia*) tend to associate with *C. racemosa.* Gray Dogwood forms a complete canopy that severely limits the available light and therefore the diversity of herbaceous plants. The canopy produced by Gray Dogwood allows many forest herbs to exploit this habitat, as evidenced by the higher floristic similarities with the wet northern forests and wet-mesic southern hardwoods than with more open communities (Fig. 2).

In the transition from either sedge meadow or fen, the *Cornus* shrub-carr alters the sedge peat to a finely decomposed, black muck. *Selaginella apoda* (Creeping Selaginella) thrives in this soil in the center of the clones along with *Caltha palustris* (Marsh Marigold), *Cirsium muticum* (Swamp Thistle), *Fragaria virginiana* (Wild Strawberry), *Impatiens biflora* (Touch-me-not), *Rubus pubescens* (Dwarf Red Raspberry), and *Senecio aureus* (Golden Ragwort). Around the margins of the clones where more light penetrates, *Cardamine pratensis* var. *palustris* (Cuckoo Flower), *Cypripedium reginae* (Showy Lady's Slipper), *Geranium maculatum* (Wild Cranesbill), *Trillium flexipes* (Drooping Trillium), and *Viola eriocarpa* (Smooth Yellow Violet) reach their optimum development. Four vines, *Clematis virginiana* (Virgin's-bower), *Convolvulus americanus* (Hedge Bindweed), *Cuscuta gronovii* (Common Dodder), and

Solanum dulcamara (Bitter Nightshade) frequently cover the sides and canopy of the *Cornus* clone and further decrease the amount of light entering the community.

The *Betula-Potentilla* shrub-carr is characterized by two strata of shrubs. The canopy is less dense than in the *Cornus* subtype and is dominated by *Betula pumila* (Dwarf Birch), with *Cornus stolonifera* (Red-osier Dogwood), *Salix bebbiana* (Beaked Willow), *S. lucida* (Shining Willow), and *Toxicodendron vernix* (Poison Sumac) of secondary importance. *Potentilla fruticosa* (Shrubby Cinque-foil) covers the well-lighted ground layer. (Cain & Slater, 1948, applied the name *"Betuletum pumilae potentillosum"* to a shrub-carr community at Sodon Lake in southeast Michigan with similar stratified shrub layers.) The herbaceous layer in the *Betula-Potentilla* subtype is also more diverse than in the *Cornus* subtype. Important members of this community are *Asclepias incarnata* (Swamp Milkweed), *Carex stricta, Chelone glabra* (Turtlehead), *Habenaria psychodes* (Purple-fringed Orchid), *Ribes hirtellum* (Low Wild Gooseberry), *Smilacina stellata* (Starry False Solomon's-seal), and *Viola cucullata* (Marsh Violet). The *Betula-Potentilla* shrub-carr has some floristic affinity with wet northern forests and sedge meadows (Fig. 2).

The *Toxicodendron-Osmunda* shrub-carr is found in drier, more acid sites, including the slope on the northern border of the study area, and in moist, acidic, sandy areas near the southern border. Large, multi-stemmed *Toxicodendron vernix* (Poison Sumac) shrubs and occasionally *Ilex verticillata* (Winterberry) or *Vaccinium corymbosum* (Northern Highbush Blueberry) are scattered over these sites with mounds of *Osmunda cinnamomea* (Cinnamon Fern) and *O. regalis* (Royal Fern) dominating the areas between the shrubs. Other noteworthy plants in the herbaceous layer include *Asplenium platyneuron* (Ebony Spleenwort), *Krigia biflora* (Dwarf Dandelion), *Lycopodium flabelli-forme* (Running Pine), *L. obscurum* (Ground Pine), and *Lygodium palmatum* (Climbing Fern). The Climbing Fern, the most unusual plant in the entire wet-land complex, has been recorded in Michigan only from this shrub-carr community in the Gourdneck State Game Area (Pippen, 1966). The southern affinity of the Climbing Fern is evident since the closest recorded location is 250 miles away in southern Ohio. Even though it is well north of its usual range, the single population of *L. palmatum* thrives in the moist acidic soil of the *Toxicodendron-Osmunda* community. Due to its proximity to and apparent intergradation with wet-mesic hardwoods, the *Toxicodendron-Osmunda* shrub-carr is slowly being invaded by both aspens and birch. This is reflected in that this unusual shrub-carr community has its only substantial floristic affinity with the wet-mesic southern hardwoods (Fig. 2).

Wet Northern Forest

Conifer swamps in the southern Great Lakes region are largely covered by tamarack forest with the herbaceous and shrub strata typical of more northern regions. Since their floristic affinity is obviously with northern lowland forests, southern tamarack forests are frequently considered to be relic outliers of wet northern forest (Curtis, 1959). The wet northern forest communities in the wet-

land complex are most frequent on solid peat, but isolated stands occur on more decomposed or mineralized muck soils. *Larix laricina* (Tamarack) forms solid stands broken up only by isolated individuals of *Acer rubrum* (Red Maple), *Carpinus caroliniana* (Blue Beech), *Cornus florida* (Flowering Dogwood), *Prunus serotina* (Wild Black Cherry), or *Toxicodendron vernix* (Poison Sumac). A well-developed and diverse shrub layer exists with *Lindera benzoin* (Spicebush) and *Toxicodendron vernix* most prominent. Other shrubs important in the tamarack swamps include *Amelanchier intermedia* (Juneberry), *Aronia prunifolia* (Red Chokeberry), *Cornus alternifolia* (Alternate-leaved Dogwood), *C. stolonifera* (Red-osier Dogwood), *Nemopanthus mucronatus* (Mountain Holly), and *Vaccinum corymbosum* (Northern Highbush Blueberry). Two interesting features of the shrub layer can be pointed out: First, a large number of dead Tamarack saplings are found in the shrub layer due to the extreme shade-intolerance of this dominant canopy member. Second, an unusually high percentage (67%) of the shrub species are berry-producers. Curtis (1959) described a similar situation in Wisconsin wet northern forests but offered no explanation.

The herbaceous layer is best represented by *Maianthemum canadense* (Wild Lily-of-the-Valley), *Parthenocissus quinquefolia* (Virginia Creeper), *Rubus pubescens* (Dwarf Red Raspberry), *Thelypteris palustris* (Marsh Fern), and *Toxicodendron radicans* (Poison Ivy). Many of the herbs, including *Carex leptalea*, *Cypripedium acaule* (Stemless Lady's Slipper), *Dryopteris cristata* (Crested Shield-fern), *Galium boreale* (Northern Bedstraw), *Trientalis borealis* (Star Flower), and *Viola pallens* (Smooth White Violet), have northern affinities. Mounds of *Sphagnum* scattered throughout the tamarack swamps are mostly confined to the bases of mature Tamaracks. Several species of true mosses and liverworts, including *Aulacomnium palustre*, *Brachythecium curtum*, *Conocephalum conicum*, *Mnium punctatum*, and *Thuidium delicatulum*, are present and sometimes abundant in these wet northern forests.

The floristic affinity of wet northern forests to fen, sedge meadow, and *Typha-Scirpus* emergent aquatic communities is evident (Fig. 2) and perhaps can be explained by mutual requirements for alkaline peaty soils. The fact that several of the wet northern forest stands are invading these other communities further indicates the ecologic and floristic similarities of these communities to the herbaceous layer of the wet northern forests.

Wet-Mesic Southern Hardwoods

The wet-mesic southern hardwood community is of minor importance in the wetland. This lowland hardwood forest community, composed mainly of *Quercus rubra* (Red Oak) and *Q. palustris* (Pin Oak), is located on moist sites adjacent to the oak forests on the northern and southern borders of the study area. *Betula alleghaniensis* (Yellow Birch), *Populus tremuloides* (Trembling Aspen), and *Sassafras albidum* (Sassafras) are of secondary importance. These lowland forest sites grade into shrub-carr or sedge meadow and therefore share a large number of herb species with both types. Some of the more typical herbs are *Carex lacustris*, *C. pensylvanica*, *Galium aparine* (Cleavers), *Impatiens biflora* (Touch-me-not), *Menispermum canadense* (Moonseed), *Monotropa uniflora* (In-

dian Pipe), *Osmorhiza claytonii* (Sweet Cicely), *Podophyllum peltatum* (May Apple), *Ranunculus abortivus* (Small-flowered Crowfoot), and *Smilax herbacea* (Carrion-flower). The wet-mesic southern hardwoods are somewhat similar floristically only to the other tall shrub or tree communities–*Cornus* shrub-carr, *Toxicodendron-Osmunda* shrub-carr, and wet northern forest (Fig. 2).

Smilax herbacea, rare in Michigan, has been recorded only from Kalamazoo and Wayne Counties. A large population of this carrion-flower grows in one of the lowland forests. No flowers were produced during the two years the population was observed. It is noteworthy that most of the specimens of this dioecious species collected by the Haneses in Kalamazoo County are sterile.

SUMMARY

Aerial photographic interpretation and vegetational analysis of the heterogeneous Hampton Creek wetland complex reveal the presence of seven community types—emergent aquatic, southern sedge meadow, fen, wet-mesic prairie, shrub-carr, wet-northern forest, and wet-mesic southern hardwoods. Indices of similarity also reveal the presence of three sub-types within the emergent aquatic and the shrub-carr communities. The extreme heterogeneity of the complex and the presence there of a number of rare or threatened species indicate a need for preservation and management.

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A COMPARISON OF VEGETATION PATTERNS IN TWO ADJACENT BOGS IN SOUTHWEST MICHIGAN

Janet R. Keough[1] and Richard W. Pippen

Dept. of Biology
Western Michigan University
Kalamazoo, 49008

Northern Michigan peatlands have been described in detail (Gates, 1942; Vitt & Slack, 1975), but those south of the "tension zone" have received limited attention. Brewer (1966), Crow (1969a, b, c) and Grant & Thorne (1955) provide descriptions of bog floras in the southern part of once-glaciated North America. These wetlands serve as refugia for unique and interesting floral communities, many species of which are considered rare, threatened, or otherwise noteworthy. Less is known about chemical interactions between peatlands and adjacent areas. This investigation of the vegetation of two adjacent bogs in southwestern Michigan was undertaken as part of a study of the movement of water out of peatlands and its possible effect on surrounding groundwater.

The wetlands, in Sections 18 and 19 of Portage Township, Kalamazoo Co. (T3S, R11W), are situated in the drainage basin and near the headwaters of the main branch of Portage Creek and not far (< 4 km.) from the drainage divide between the Kalamazoo and St. Joseph River basins. The watershed enclosing the wetlands drains directly into a tributary, Hampton Creek, and Hampton Lake, which is an alkaline lake downstream. The glacial debris surrounding the wetlands has been described as outwash plain layered with till (Passero et al., 1978). The bogs are "down-wash" from the Outer Kalamazoo Moraine; this area was probably one of high activity during the last Wisconsinan recession, as the stratigraphy is a complex of sandy outwash with discontinuous layers of till and alluvial deposits. The area encompassing and including the wetlands slopes gradually from north to south. Peat borings indicate that the wetlands are located in a series of basins, depths of which suggest ice-block depressions, or kettles. The large bog on the north side occupies three basins which are 6.6 m., 8.6 m., and 6.5 m. in depth. The small bog on the south side of the area is situated in a basin 6.6 m. deep (Fig. 1). The two bogs, referred to henceforward as the North and South Bogs, are 250–300 m. apart and are separated by and situated north and south of a major thoroughfare. Presumably, they have experienced similar glacial and climatic histories.

The North Bog is privately owned and is partially surrounded by a developing commercial recreation area; sections of a golf course (appropriately named The Moors of Portage) lie along parts of the lagg. The South Bog is privately owned in part, but approximately half lies within the Michigan Dept. of Natural Resources Gourdneck Game Area. The Game Area includes a number of fens, including Hampton Creek Fen, wet prairies, and other wetlands, as well as

Fig. 1. Topographic map of the study area indicating peat depth contours (derived in part from Kalamazoo Co. Planning Council, 1978).

uplands. Together, these areas harbor several floral communities and many rare, threatened, and otherwise noteworthy species (Sytsma & Pippen, ms.; Pippen, 1976). The peatland vegetation groups studied here contrast strikingly with these diverse communities.

Line transects were established across the North Bog from north-to-south and east-to-west. Each transect was divided into 20 m. sections, and one 25 m^2 quadrat (5 m. X 5 m.) was selected at random within each for the vegetation analysis. In all, information from 143 quadrats was combined to characterize the vegetation of this site.

Since the South Bog is significantly smaller and more regular in shape, and its vegetation appears to vary in concentric zones, line transects radiating from the center were selected. A randomly selected compass bearing was used to divide the nearly circular wetland into four equal quarters. Within each quadrant, one radius was selected at random to locate a line transect. The vegetation was assessed using quadrats placed along these four radial transects. In the central forested area, two points were located randomly along each radius, and one 25 m^2 and one 100 m^2 nested quadrat were evaluated at each point. Data from the eight samples were combined. Shrubby and herbaceous communities form zones which ring the central forest. To characterize these zones, contiguous m^2 quadrats alternating left and right along each radial transect line were examined from the forest edge to the lagg. The "shrub zone," defined as the zone dominated by woody plants under 1.5 m tall, occurred in 48, 18, 22, and 24 quadrats (112 total) along the four radiating line transects and adjacent to the forest; the surrounding herbaceous zone was represented by 8, 18, 11, and 4 quadrats (41 total) on the same transects, but outside the shrub zone. Only species presence was recorded for all quadrats; density and cover were deemed too difficult to measure accurately or consistently for multistemmed shrubs, sedges, many herbs, or mosses. Voucher specimens were deposited in the Hanes Herbarium at Western Michigan University. Moss samples identified by Dr. Howard Crum were deposited at the University of Michigan Herbarium.

Wetland area was measured on 1977 USDA aerial photographs with a Bruming Areagraph Chart (100 dots/in.^{2}). Peat depths were determined using a Davis peat borer. The pH of surface waters was determined with a Fisher Acumet pH meter. Standard survey techniques, using alidade and plane table, were employed to determine the relative elevations of the wetland surfaces.

Both wetlands are completely underlain by peat, waters are acidic (pH = 4.5−5.5), species of *Sphagnum* cover the vegetated area, and other typical bog vegetation, especially ericaceous species, dominate the understory and canopy; these are typical characteristics of bogs (Golet & Larson, 1974; Jeglum et al., 1974). The vegetation, including the moss layer and saturated peat surface, of each bog was found to be "perched" above the surrounding lagg and ground water. The species composition of both sites is relatively depauperate; fewer than 50 species of vascular plants were found during two field seasons.

The North Bog lies "above" the South Bog at 265 m. elevation (the latter is at 263.6 m.). This wetland, 10.3 hectares (25.5 acres) in size, is covered by *Chamaedaphne calyculata* (leatherleaf) (frequency = 0.98) and hummocks of *Sphagnum* spp. (freq. = 1.00). Secondary species, such as *Carex oligosperma* (0.36), *Eriophorum virginicum* (cotton grass) (0.34), *Woodwardia virginica* (Virginia chain fern) (0.14), *Acer rubrum* (red maple) (0.02), *Andromeda glaucophylla* (bog rosemary) (0.13), and *Vaccinium corymbosum* (high bush blueberry) (0.05), occur in small patches throughout the wetland. There are a few pitcher plants (*Sarracenia purpurea*) near the center, and Michigan Holly (*Ilex verticillata*) and chokeberry (*Aronia melanocarpa*) occur sparsely. Throughout the area, *Vaccinium oxycoccus* (cranberry) and *Polytrichum juniperinum*

var. *affine* (hair-cap moss) are frequent on the tops of hummocks (frequencies of both = 0.30 (Table 1; Figs. 2, 4, 5).

Two areas in the large wetland are radically different; the north and west tips are dominated by aquatic vegetation—mainly *Nuphar advena* (yellow water lily) in perennially standing water. Presumably, relatively mineral-rich groundwater enters the peatland through these areas. The entire wetland is surrounded by a lagg, variously bordered to the outside by *Calamagrostis canadensis* (blue joint), *Glyceria grandis* (manna grass), *Phalaris arundinacea* (reed canary grass), *Ilex verticillata,* and *Vaccinium corymbosum.* A small area of open water remains within the bog near the southeast side (Fig. 2); this is surrounded by a floating mat of *Sphagnum* spp. and leatherleaf.

The South Bog, of 2.2 hectares (5.34 acres), differs somewhat from the North Bog community (Table 1). The center is heavily forested with *Aronia melanocarpa* (frequency = 1.00), *Nemopanthus mucronata* (mountain holly) (1.00), *Vaccinium corymbosum* (1.00), *Rhamnus frangula* (buckthorn) (0.88), and *Larix laricina* (tamarack) (frequency = 0.88, mean d.b.h. = 9.4 cm, or 3.7 in.). Mountain holly occurs only rarely in this part of Michigan, near the southern edge of its range (Pippen, 1976). The understory shows frequencies of *Woodwardia virginica* (1.00), *Ilex verticillata* (0.50), *Acer rubrum* (0.38), *Carex*

TABLE 1. Frequency of woody and herbaceous species.

	NORTH BOG		SOUTH BOG	
	Shrub mat	Central Forest	Peripheral Shrub zone	Peripheral Herbaceous zone
Woody species				
Acer rubrum	0.02	0.38		
Andromeda glaucophylla	0.13			
Aronia melanocarpa		1.00	0.29	0.16
Chamaedaphne calyculata	0.98	0.38	0.91	
Ilex verticillata		0.50		
Larix laricina		0.88		
Nemopanthus mucronata		1.00		
Rhamnus frangula		0.88		
Toxicodendron vernix		0.13		
Vaccinium corymbosum	0.05	1.00		
Herbaceous species				
Carex oligosperma	0.36	0.38		0.17
Dulichium arundinaceum	0.02	0.16	0.16	0.47
Eriophorum virginicum	0.34	0.13	0.08	
Glyceria grandis				0.67
Polytrichum juniperinum var. affine	0.30			
Sphagnum spp.	1.00	1.00	1.00	1.00
Vaccinium oxycoccus	0.30			
Woodwardia virginica	0.14	1.00	0.66	0.35
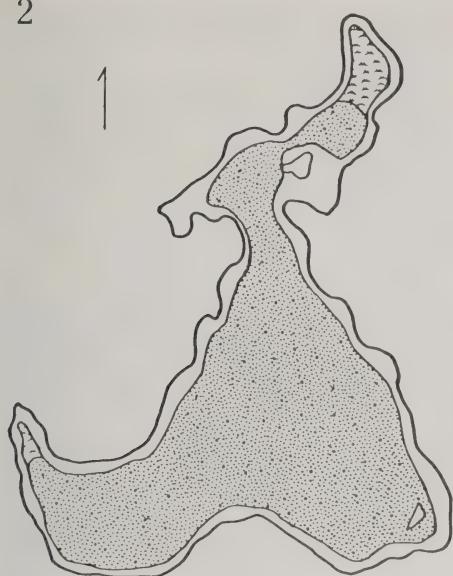
Fig. 2. Vegetation map of North Bog.   Fig. 3. Vegetation map of South Bog.

oligosperma (0.38), *Chamaedaphne calyculata* (0.38), *Eriophorum virginicum* (0.13), and *Toxicodendron vernix* (poison sumac) (0.13). *Sphagnum* spp. provide a complete ground cover (frequency = 1.00).

A zone dominated by *Chamaedaphne calyculata* (frequency = 0.91) surrounds the central forest; less frequent species include *Woodwardia virginica* (0.66), *Aronia melanocarpa* (0.29), *Dulichium arundinaceum* (three-way sedge) (0.16), *Eriophorum virginicum* (0.08), and *Carex oligosperma* (0.05). *Sphagnum* spp. underlie this zone as well (frequency = 1.00).

An area nearly devoid of woody plant species extends around most, but not all of the perimeter. *Glyceria grandis* (frequency = 0.67), *Dulichium arundinaceum* (0.47), *Woodwardia virginica* (0.35), and *Carex oligosperma* (0.17) are the most common members of this community; as an exception, the woody *Aronia melanocarpa* is relatively abundant (frequency = 0.16). Species such as *Carex canescens, Eleocharis obtusa, E. robbinsii, Iris virginica* (blue flag), *Rumex crispus* (curly dock), and *Scirpus cyperinus* (wool grass) occur sparsely in patches. *Sphagnum cuspidatum* is the most common (if not the only) moss, occurring in standing water throughout the zone. Like the large bog, this wet-

land is entirely surrounded by a lagg, in which both *Riccia fluitans* and *Ricciocarpus natans* (aquatic liverworts) flourish, as well as species of *Spirogyra,* which form an extensive mass on the moat surface (Figs. 3, 6, 7).

Samples of *Sphagnum* were collected from various microhabitats within the two sites. Four species were found regularly. *S. cuspidatum,* as stated earlier, occurs in standing water within and near the lagg and between hummocks in saturated conditions. *S. magellanicum* and *S. capillifolium* occur in drier situations—on hummock tops, often with *Vaccinium oxycoccus*—and form hum-

Fig. 4. Vegetation of North Bog as viewed from the air. Fig. 5. Vegetation of the North Bog as viewed from the southwest edge.

Fig. 6. Vegetation of South Bog as viewed from the air.

mocks about the bases of *Larix* and *Chamaedaphne*. Three variants of *S. recurvum* were found to occupy intermediate moisture regimes; *S. recurvum* var. *brevifolium* occurs in rather wet conditions around the bases of *Chamaedaphne, Larix,* and *Vaccinium corymbosum*. *S. recurvum* var. *recurvum* locates in somewhat drier conditions, near the bases of *Acer rubrum, Vaccinium corymbosum*, and *Nemopanthus mucronata,* and *S. recurvum* var. *tenue* occurs on low hummock tops. The distribution of these species agrees well with the descriptions of hummock-hollow zonation by Vitt et al. (1975) and the habitats of *Sphagnum* spp. as outlined by Crum (1976).

The two bogs are part of an extensive complex of peatland and upland habitats, all on substrata exposed at the same time by receding glaciation. The Hampton Creek wetland, which is located in the same drainage basin, is composed of a complex of emergent aquatics, southern sedge meadow, fen, wet-mesic prairie, shrub carr, wet northern forest, and wet-mesic southern hardwood forest. Peat in the wetland portion of this area is less than 3.6 m in depth, and waters are considerably more nutrient-rich; pH ranges from 6.3–7.1, and alkalinity averages 220 mgl^{-1}. The flora is exceedingly diverse. In all, 373 species of vascular plants were found; in the wet meadows alone 105 species reached frequencies greater than 0.05 (Sytsma & Pippen, *ms.;* Pippen et al., 1979). Curtis (1959) found 115 species in fens and 197 species in southern sedge meadows studied for the P.E.L. continuum analysis.

The two bogs contrast strikingly with these wetland communities. Peat is deeper (reflecting basin depth as well as drainage and decomposition rates), and the ionic content of water is low and more acidic. Fewer plant species inhabit these bogs. The vegetation is clearly affected by the predominance of *Sphagnum* and the peat substrate, which, in turn, are controlled by and serve to enhance

low groundwater flow. The unique characteristics of bogs (notably in vegetation and water chemistry) are the result of the collective effects of climate, glacial history and remaining debris, basin morphometry, groundwater flow, and colonization by acid-producing species, such as *Sphagnum.*

The two bogs provide an opportunity to observe trends in vegetation communities in peatlands and to explore reasons for differences in vegetation

Fig. 7. Vegetation of South Bog as viewed from the west edge outside the lagg.

pattern. The North Bog occupies three basins, one of which still has a remnant of open water. It is covered with shrubby vegetation, noticeably without forest canopy, at present and presumably also in the past, although small individuals of *Acer rubrum* occur sparsely, usually near the basin divides within the bog. The South Bog is considerably smaller and apparently occupies a single basin. The forest in the center is well developed. The *Chamaedaphne*-dominated shrub community ringing the forest suggests that this association may have prevailed in the central portion, as well, at an earlier time. The two wetlands' proximity, peat depths, and similar surrounding glacial material and topography strongly suggest that they experienced similar conditions throughout their histories.

The explanation for the different nature of the vegetation of the two can only be speculative. Difference in size may be a critical factor. A small basin may fill more rapidly, thus allowing for increased compaction in the center, more rapid lifting of the peat surface, and the invasion of tree species. One of the three basins of the North Bog is not yet filled to the surface, as evidenced by the remaining open water. This deep basin may be controlling (slowing) vertical peat development in other areas of this wetland. One cannot rule out the possibility of some past catastrophic event, such as fire, which may have removed trees from the North Bog, although no stumps or logs—evidence of a former canopy community—were found in the bog. Another parameter known to affect peatland change is groundwater flow. The entire area slopes gradually from north to south. Boelter & Verry (1977), Bay (1967), and others have suggested that the waters of seemingly ombrotrophic bogs (strongly acidic and with the "correct" species) may, to some extent, interact with surrounding groundwaters. If acidic water from the North Bog is moving out of the basin, it is probably moving south toward the South Bog. Thus, the South Bog may receive considerably lower concentrations of dissolved ions and so experience conditions much more conducive to peat development. Heinselman (1970) suggested that peat accumulation may be more rapid in infertile sites. Circulation of water can affect bog development. Although generally slow, due to low slope and compacted peat, any movement of water through the North Bog, especially near the surface, may be greater than that through the South Bog, as a result of the relatively greater compaction and the convex nature of the latter's surface. This discussion is only one suggestion among others attempting to explain why the different peatland communities exist as we see them today.

SUMMARY

As part of a study related to bog hydrology and development, the floristics of two adjacent bogs in southwestern Michigan were investigated. The North Bog is dominated by *Sphagnum* spp. and *Chamaedaphne calyculata* and has no significant forest canopy. This is a large wetland, occupying three basins, one of which is still occupied by standing water. The South Bog bears a central forest of *Larix laricina, Nemopanthus mucronata, Aronia melanocarpa, Rhamnus frangula,* and *Vaccinium corymbosum.* Roughly concentric rings of shrubby vegetation (mainly *Chamaedaphne*) and herbaceous vegetation (mainly *Dulichium arundinaceum, Glyceria grandis,* and *Woodwardia virginica*) encircle the forest. Speculation is made on the differences between the vegetation patterns of the two wetlands which are in close proximity and have probably experienced similar glacial and climatic histories. Size, basin depth, and groundwater chemical composition and flow rates are suggested as probable controls over the development of peat and the invasion of tree species.

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A REVIEW OF THE OCCURRENCE OF HALOPHYTES IN THE EASTERN GREAT LAKES REGION

P. M. Catling and S. M. McKay

Dept. of Botany
University of Toronto
Toronto, M5S 1A1
Ontario, Canada

Salt-tolerant plants are characteristic of the sea coast (Duncan, 1974) and have long been known in the interior of western North America (Steyermark, 1940; Ungar, 1974; Nelson, 1979). Various authors have discussed the salt marsh vegetation of the Hudson and James Bay areas (Schofield, 1959; Kershaw, 1976; Riley & McKay, 1980; Ringius, 1980), and Rousseau (1974, p. 484) has listed the halophytes of Quebec and discussed some of them in detail. Peattie (1922) and Guire & Voss (1963) have drawn attention to the occurrence of maritime plants (psammophytes rather than halophytes) around the Great Lakes shores. Svenson (1927) discussed the possible influence of post-Pleistocene submergence on the occurrence of both psammophytes around the Great Lakes and halophytes in western New York. He concluded that halophytes may have been introduced into the Great Lakes region by the brackish Champlain sea (in the upper St. Lawrence-lower Ottawa valley), but there is no convincing evidence for this. Many of the halophytes do not occur as far north as the Gulf of St. Lawrence and could not have followed salt water into the eastern Great Lakes region any other way (Svenson, 1927, pp. 111–112; see also maps of glacial lakes phases during Wisconsinan recession in Prest, 1970). Svenson (1927) wrote that the origin of the halophytic flora of the Great Lakes "appears to be complex involving not only the question of post-Pleistocene submergence but also the question of post-glacial migrations from the west, and of . . . transportation by human agencies." The presently observable tendency for many halophytic plants (see table 1) to be restricted to habitats with abnormally high sodium salt levels suggests that if any were native inland in the northeast, there must have been some naturally occurring sodium-rich habitats. Any indication of halophytes in a natural sodium-rich habitat before the development of the local extractive salt industry would provide satisfactory evidence of native occurrence. More or less distinctive varieties of certain species have been described from one or more estuary systems along the Atlantic coast. Brackish situations in the eastern Great Lakes region are even more isolated, especially with respect to pre-adapted halophytes. Considering the possible occurrence of adapted ecotypes or local endemics, these inland brackish areas may be of interest from an evolutionary point of view. The apparently recent spread of halophytes along highways in the northeast is of ecological interest with respect to which species are involved and why and of practical interest with respect to the maintenance of roadside vegetation.

In an attempt to document the occurrence and status of halophytes in the eastern Great Lakes region we have collected and summarized all references to

halophytic plants and sodium-rich substrates. The questions of natural versus man-made habitats and native occurrences versus recent spread have been considered in detail. A literature search was made to find references to natural salt springs and halophytes, particularly those plants invariably associated with high levels of Na-salt (table 1) occurring in the eastern Great Lakes region. Other halophytic plants which are not always associated with Na-salt have also been considered. The records and diaries of early botanical explorers and surveyors have been examined for clues as to native occurrence. Various salt companies, historians, local botanists, and herbarium curators were contacted for information regarding natural salt springs and early records of halophytes and Na-rich habitats.

TABLE 1. Halophytes recorded inland in the northeast, generally restricted to habitats with abnormally high sodium salt levels.

Ruppia maritima	*Juncus compressus*
Muhlenbergia asperifolia	*J. gerardii*
Spartina patens	*Chenopodium rubrum*
Diplachne acuminata (=*Leptochloa fascicularis* v. *acuminata, L. acuminata*)	*Atriplex argentea*
	Salicornia europaea
Diplachne maritima (=*Leptochloa fascicularis* v. *maritima*)	*Suaeda calceoliformis* (= *S. depressa*)
	Spergularia marina
Poa arida (incl. *P. glaucifolia*)	*S. media*
Eleocharis parvula (=*Scirpus nanus*)	*Solidago sempervirens*
Scirpus olneyi	*Aster brachyactis*
S. paludosus var. *maritimus* (=*S. maritimus*)	*A. subulatus*
Carex praegracilis	*Pluchea purpurescens*

New York State

In the Syracuse-Onondaga Lake area of central New York, there is reliable evidence for the presence of sodium salt springs and water with high sodium levels prior to settlement by European people. In 1654 a Jesuit missionary reported: "We arrive at the entrance to a little lake in a great basin that is half dried up, and taste the water from a spring of which these people dare not drink, as they say there is an evil spirit in it. I find it to be a spring of salt water; and indeed we made some salt from it, as natural as that which comes from the sea" (LeMoine in Thwaites & Kenton, 1925, p. 256). Later reports of Jesuits and other early explorers in this area (*e.g.* Bartram, 1751, pp. 45 and 55) refer to the ready-made salt crystals on the soil near the springs and the ease with which salt could be obtained by boiling the water. The manufacture of salt from the Onondaga salt springs on a commercial scale began in 1789. Munson (1969, pp. 67–68) reported that girls "gathered the tiny samphire plants—new-green in the spring, bright red in autumn—that grew in the salt marsh; they made a tasty salad eaten raw, or a 'mess of greens' when boiled with a bit of pork." This was apparently about 1798. The local salt industry was well established by 1792. Thus the seed may have been introduced with salt-making equipment brought from the Atlantic coast.

In 1807, seventeen years after the start of commercial extraction of salt, Frederick Pursh visited the Onondaga salt springs (McVaugh, 1935). It is surprising that Pursh did not collect any obligate halophytes in the area. Although most of his collections from the springs were made in mid-July, he was at Onondaga until mid-August, at which time any local halophyte flora should have been well developed.

The reference to "samphire" in 1798 (shortly after the establishment of the industry) and the occurrence of an appropriate habitat prior to the industry is the best evidence for native halophytes in the region. Since *Salicornia europaea* does show up now in sites recently made saline, as in Ohio (Cusick, 1970), Illinois (Swink & Wilhelm, 1979), and elsewhere in New York (Muenscher, 1927b), it may have done so then. Thus the question of native occurrence of halophytes at Onondaga Lake is not entirely settled. It does, however, seem likely.

Paine (1865) reported that *Salicornia europaea* was common at Salina and abundant on the west side of the lake opposite Liverpool, much of the lower ground being covered with it. He believed that the presence of *Ruppia maritima* in Onondaga indicated previous connection with the sea. Other species reported from the alkaline marshes about Onondaga Lake include *Najas marina* (as *N. major*), *Zannichellia palustris, Triglochin maritimum, Panicum dichotomiflorum* (as *P. proliferum*), *Diplachne maritima* (as *Leptochloa fascicularis*), *Scirpus maritimus, Juncus gerardii* (as *J. bulbosus*), *Chenopodium rubrum* (as *Blitum maritima*) and *Atriplex patula* var. *hastata* (Clinton, 1865; Drummond, 1864, 1867; Paine, 1865). Later Goodrich (1912) reported collections of *Spergularia marina, Spartina patens,* and *Puccinellia distans* and noted an abundance of *Juncus gerardii* in the area. John Yuhas (1975) and M. E. Faust (1977, pers. comm.) considered various halophytes native to the Onondaga Lake area and indicated that they had been depleted and were endangered. Apparently once extensive, the Onondaga salt marshes have been drastically reduced by filling and development.

Halophytic plants were very likely native elsewhere in New York State. Dudley (1886, p. xix) quoted a Jesuit missionary who described the capture of large numbers of "pigeons" at the "salt springs" on the west side of the Cayuga marshes in 1671. This reference to salt springs apparently antedated any salt industry in the area. At the adjacent Montezuma marshes Dudley (1886) reported *Zannichellia palustris, Panicum dichotomiflorum* (as *P. proliferum*), *Diplachne maritima* (as *Leptochloa fascicularis*), *Scirpus maritimus, Juncus gerardii, Atriplex patula* var. *hastata, Chenopodium rubrum,* and *Ranunculus cymbalaria. Najas marina* was reported from Cayuga Lake.

Spergularia alata Wieg. was described as a new local endemic from the salt flats east of Montezuma village and from Salt Pond west of Howland Island (Wiegand, 1920). Later this taxon was incorrectly placed in synonymy with *S. media* (L.) Presl. (Rossbach, 1940, p. 123; Fernald, 1950), the error apparently resulting from Wiegand's (1920, p. 16) emphasis on differences other than the number of stamens, but Wiegand's (1920) description does indicate that *S. alata* has 4–6 stamens. Our examination of numerous topotypes collected in 1979 indicated 2–4 stamens. The number of stamens is a basic feature

in the classification of North American *Spergularia.* Rossbach's (1940) key gives 6–10 stamens for *S. media* and 2–5 for *S. marina.* In her text, she gives 9–10 stamens for *S. media* and 2–5 stamens for *S. marina.* Various manuals on the northeastern flora make a similar distinction. Thus on the basis of stamen number (in the original description and in topotypes) *S. alata* is not a synonym of *S. media.* In the possession of uniformly winged seeds, *S. alata* differs from the type of *S. marina* (Rossbach, 1940) although Rossbach admits that *S. marina* occasionally has a "white, usually erose wing which may be as broad as 0.4 mm." Since plants with papillose seeds appear to intergrade with smooth-seeded plants (*S. leiosperma,* see Fernald & Wiegand, 1910) and plants with winged seeds also intergrade with smooth-seeded plants, both the latter seed types sometimes occurring together in a capsule (see Rossbach, 1940; Catling & McKay, 1980), it seems undesirable to recognize these extremes of seed types without some detailed study. Although Rossbach (1940) could not accept the formal taxonomic rank for the plants with smooth seeds, she apparently paid little attention to plants referable to *S. marina* with winged seeds. For the time being, *S. alata* seems best considered as part of *S. marina,* but there is a need for some research that may elevate it again to the status of a local endemic or perhaps to a more widespread taxon with some other name. Thus the type locality in the Montezuma marshes, where these plants still occur, assumes some significance.

Wiegand & Eames (1925, p. 456) listed a group of "salt plants" which are nearly all confined to the Ontario Plain and adjacent parts of the lake valley in New York State. Some species were said to be "plainly influenced by the salt," while others, less closely associated with the salt springs, could not be clearly associated with the salt. Additions to Dudley's list of "salt plants" included *Triglochin maritimum, Phragmites communis, Spartina pectinata, Hierochloe odorata, Zizania aquatica, Eleocharis parvula* (as *Scirpus nanus*), *Eleocharis rostellata, Juncus dichotomus* var. *platyphyllus,* and *Spergularia marina* (as *S. alata*). *Salicornia europaea, Juncus compressus,* and *Puccinellia distans* were reported as "adventive" (Wiegand & Eames, 1925). Both Dudley (1886) and Wiegand & Eames (1925, *e.g.,* see under *J. gerardii,* p. 139) considered the "salt plants" to be native to the region.

In the marshes east of Montezuma there are still areas dominated by *Juncus gerardii* with some *Scirpus maritimus* var. *paludosus* and *Spergularia marina* on mud flats. Salt Pond west of Howland Island near Savannah is intact and has *Spergularia marina* and *Atriplex patula* var. *hastata* on clay around alkaline pools beyond which is a zone of *Spartina pectinata* and *Hordeum jubatum* with scattered *Lythrum salicaria* and *Scirpus olneyi* in wetter places (Fig. 1). Salt Pond appears to be a natural alkaline site (judging from the fact that *Puccinellia distans* is conspicuously absent). Local residents report that Indians made salt there, and so did early residents, but there was never a well-developed industry. Wells drilled to a depth of 40 feet on higher ground one-quarter of a mile from Salt Pond are said to yield salt water.

Clausen (1949) added to the list of halophytes of the Cayuga region *Aster brachyactis* and *Spergularia media,* both species undoubtedly representing recent introductions.

Halophytes (including *Ruppia maritima, Juncus gerardii, Spartina patens,* and *Salicornia europaea*) have been recorded along Wolf Creek between Silver

Fig. 1. Salt Pond west of Howland Island in the Montezuma marshes (Wayne Co., N. Y.) with *Spergularia marina* and *Atriplex patula* var. *hastata* on Na-rich clay around edges of pools and a surrounding zone of *Spartina pectinata, Hordeum jubatum,* and *Scirpus olneyi.*

Springs and Castile in Wyoming Co. (Muenscher 1927a,b; Zenkert, 1934, p. 307). Their presence along the marshy shores of the creek has been attributed to waste discharged from the salt factory at Silver Springs.

Michigan

Scirpus olneyi, with both coastal and midwestern affinities, was collected in 1837 in the vicinity of a "saltworks" in southern Gratiot Co. where it was relocated in 1960 (McVaugh, 1970). Houghton (1838) reported brine springs at several places along the Maple River in Clinton and Gratiot Counties. The saline marshes in Gratiot Co., as he described them, would appear to represent a suitable habitat for halophytic plants. He failed to mention any human presence: "Numerous small pools of brackish water are irregularly distributed over them, and the soil is apparently saturated through their whole extent with it .... These marshes are the favorite resort of wild animals, and paths, deeply worn by deer, were seen in every direction." A shaft was sunk into a spring along the Maple River in Clinton Co. shortly after Houghton's visit and perhaps McVaugh's reference (1970, p. 241) to a "salt works" refers to this. In his report Houghton (1838) did not mention any "salt works" along the Maple River, and the extraction of salt on a commercial scale in Gratiot Co. began in 1882 (Cook, 1914). Thus, *Scirpus olneyi* is probably native in this area, and the 1875 record of the mainly coastal *Eleocharis parvula* (Voss, 1972, p. 339) on brackish banks of the Maple River may also represent a native occurrence. Wheeler's (1891) report of

S. olneyi and *E. parvula* about a "deer lick" near Hubbardston, in Ionia Co., ca. 1887, may also represent native occurrences since natural brine springs were known in the general area, and we have not come across a reference to a well or salt industry at Hubbardston.

Although Houghton (1838, pp. 108–133) drew attention to several areas of natural brine springs (mostly weak) in Michigan, the only plant he mentioned in association with any of them is *Chara* (on the Grand River). Thus, the natural brine springs in Michigan appear to have had *Chara, Scirpus olneyi,* and *Eleocharis parvula,* the two latter being rare in the state.

The successful attempts at commercial extraction of salt in Michigan began at Grand Rapids in 1840, but it was not well developed at Grand Rapids and East Saginaw until ca. 1850. After this it spread to other parts of the state, and 110 companies were in operation by 1895 (Cook, 1914; Allen, 1917). Thus, to be native with certainty, a halophytic plant should have been collected before or about 1860 depending on the location.

In 1916, Farwell reported *Salicornia europaea, Aster subulatus,* and *Pluchea camphorata* from the vicinity of the saltworks at Oakwood, south side of Detroit, Wayne Co. He suggested that the occurrence of these plants was due to the water and crystals from a nearby saltworks converting the soil to an alkaline condition. Brown (1917) added *Spartina patens* to the plants found in the Oakwood area. It had previously been found in the freight yards at Port Huron in 1910 (MSC). *Juncus gerardii* has also been found in the freight yards at Port Huron (Voss, 1972). The salt industry, established at Oakwood in 1895, was well developed in the general region in the early 1900s (Cook, 1914), probably providing much artificial habitat for halophytes.

In 1799, salt from Onondaga Lake, New York, was sold at considerable profit in Detroit suggesting a lack of a local source of supply (Munson, 1969, p. 71). Nuttall (1810, *in* Graustein, 1951) noted that springs were scarce near Detroit, and although he did some water chemistry, he failed to detect any salt in a spring three miles south of the town, nor did he mention any salt springs in the area. W. A. Walden, geologist with the Michigan Dept. of Natural Resources, suggests that "the brief review of the literature covering the Detroit area does not reveal any natural salt springs in the vicinity of the southern part of Detroit" (pers. comm.). He reports however, that there were flowing wells, some of which produced salt water (Peale, 1886). Apparently these wells were numerous in the district of Ecorse prior to Brown's (1917) reports of halophytes there, but flows diminished as use of the bedrock aquifer increased, and by about the time of Brown's observations many wells had to be pumped. Walden reports that the possibility of natural salt springs is remote since the glacial sediments overlying the salt beds are of the heavy clay type and vary from 70 to 100 feet in depth. Other evidence (see under "Ontario") also indicates an absence of natural Na-salt springs in the Detroit area. However, Bela Hubbard (1839, pp. 306–7, *in* Fuller, 1928), reporting to Douglass Houghton on the geological aspects of Wayne Co., reported on the early manufacture of salt by the Indians and French from very weak brines on the banks of the Rouge River and some old maps (*e.g.* McNiff's 1790 map) indicate a salt spring on the south side of the mouth of the Rouge River, in the town of Redford, which at that time was southwest of Detroit.

Ruppia maritima, a widespread plant typically of brackish water, is apparently locally common in Manistique Lake, Mackinac Co., Michigan (Voss, 1965), where it was collected by D. E. Miller in 5—8 feet of water in 1926, E. G. Voss, C. W. Laskowski, and J. S. Russell in 1964 (MICH), and R. L. Stuckey (OS) in 1966. At this location it occurs with *Chara* (Voss, 1965), but it has not yet been associated at this site with either natural Na-salt or with the salt industry.

Reznicek (1980) recently discovered a remarkable assemblage of halo-phytes associated with the use of de-icing salt on highways. Some halophytes new to the state were thought to represent recent introduction rather than over-looked native occurrences. Reznicek (1980) suggested that on the basis of ob-vious colonizing ability and distributional history some Michigan halophytes (*Carex praegracilis, Muhlenbergia asperifolia,* and *Suaeda calceoliformis*) were likely introduced during the period of settlement by European man.

Ohio

The Indians and early settlers in Ohio concentrated salt by evaporation of natural brines issuing from certain rock formations (Stout, Lamborn & Schaaf, 1932). Apparently the salt springs ("licks") were principally in southern and eastern Ohio (H. R. Collins, state geologist, pers. comm.). The terms "lick" and "salt" are commonly used in stream names in this part of the state and usually refer to natural brines.

A salt industry was well established in Ohio in the early 1800's, using surface brines or pumping from depths of a few to several hundred feet. Be-tween 1806 and 1808, 20 furnaces were in operation at Scioto Springs near Jackson, producing 50 to 70 bushels of salt per week (Stout, Lamborn & Schaaf, 1932). When European hunters and traders first visited this part of the country, thousands of buffalo visited these springs, and the Indians boiled the brine to make salt (Hildreth, 1838; Bownocker, 1906). The Scioto Springs were among the earliest known salt springs inland west of the Appalachians and ranked with the Big Bone and Blue Licks in Kentucky for antiquity, since fossil bones of Mammoths and Mastodons were found imbedded in the mud and clay (Hildreth, 1838). Houghton (1838) also alluded to the manufacture of salt from an Ohio "buffalo-lick." The early history of salt-making from relatively shallow natural brines was outlined by Bownocker (1906).

Solid rock salt beds underlying a large portion of eastern Ohio at depths between 1,350 to 6,500 ft. (Clifford, 1973) were first discovered in 1886 near Cleveland (Lefond, 1969) and first extracted in 1889. These relatively deep salt beds are presently exploited at several localities (Stout, Lamborn & Schaaf, 1932; Lefond, 1969).

Of the halophytes listed in table 1, *Muhlenbergia asperifolia, Diplachne acuminata (sub Leptochloa fascicularis), Juncus gerardii,* and *Aster subulatus* were listed for the state by Weishaupt (1960). The earliest to be recorded in the state was *Juncus gerardii* reported from the Lake Erie shore in 1874 (see Stuckey, 1979). Collections from Cleveland in 1891 and 1895 (*E. Claassen, s.n.,* OS) did not precede the salt industry there. As a result of his detailed study,

Stuckey (1979) considered *J. gerardii* to be a "non-indigenous member of the wetland flora in isolated localities of the Great Lakes region."

Of the other species listed by Weishaupt (1960), the earliest collection records at OS are 1932 for *Aster subulatus* near oil wells at Bowling Green (*E. L. Moseley 2177.1*) and 1934 for *Diplachne maritima* (*sub Leptochloa fascicularis*) in Pickaway and Jackson Cos. (*Bartley & Pontius s.n.*). Other records (at OS) for the halophytes listed by Weishaupt are more recent and associated with roadsides, railways, and a salt mine. *Aster brachyactis* was first collected in Ohio in Ottawa Co. in 1970 (*R. L. Stuckey 9231* OS).

Cusick (1970) reported *Salicornia europaea* and *Atriplex argentea* from the environs of brine wells at Rittman in Wayne Co., Ohio; both species were new to the state. *Corispermum hyssopifolium, Cyperus esculentus, Juncus effusus,* and *Typha angustifolia* were also associated with the halophytes at this site. The manufacture of salt by the Ohio Salt Co. at Rittman began in 1898 (Stout, Lamborn & Schaaf, 1932).

Riehl & Ungar (1980) reported *Spergularia marina* from the vicinity of a salt factory and suggested recent introduction. A number of both eastern and western halophytes have recently been discovered by R. J. Bartolotta and J. Bissell in and near Painesville Township, Lake Co. (R. L. Stuckey, pers. comm.). These occurrences are apparently associated with the brine fields (Clifford, 1973) since we are unaware of any local record of natural salt springs. Nuttall (1810 *in* Graustein, 1951, p. 48) described sand plains about Painesville but made no reference to salt or halophytic plants.

If halophytic plants were native in Ohio, this can only be proven with specimens collected before 1800, since the salt industries were widespread and well developed shortly after that time. No such specimens are known to the authors, nor are we aware of any references to the flora associated with the natural salt springs. A survey of any natural springs still in existence and undisturbed in the past may help to establish whether or not there are native halophytes.

Ontario

In Ontario all references to "salt springs" that we have investigated have referred to $CaCO_3$ rather than Na salts, and the brine and rock salt deposits are so deep (Hewitt, 1962) that naturally occurring springs are very unlikely. We have not come upon any evidence for salt at the surface prior to the local extractive salt industry.

The salt industry was well developed in Ontario by the late 1800s and early 1900s. The first well was drilled at Goderich in 1880; production at Windsor began in 1893 and at River Canard in 1919 (Hewitt, 1962). In addition to alkaline habitats about brine wells and salt factories, brine sometimes originated from the many oil wells in southwestern Ontario.

The earliest occurrences of halophytes in Ontario include various "non-obligate" species (*Puccinellia distans* and *Atriplex patula* var. *patula,* var. *hastata,* and var. *littoralis*) collected in the late 1800s and early 1900s from various cities (Ottawa, London, Toronto, and Sarnia). The earliest records of halophytes that

are generally confined to Na-rich sites include W. Scott's collections of *Aster brachyactis* and *Juncus gerardii* in 1903–4 from the railway yards at Niagara and Montrose (TRT). These early records also represent a period when man-made Na-rich habitats were widespread. Almost all records of obligate halophytes are recent.

Halophytes associated with the use of de-icing salt at Toronto were described in 1975 (by Catling & McKay). The recently adventive (in Ontario) *Carex praegracilis* has been associated with relatively high levels of Na along major highways (Reznicek, Catling & McKay, 1976). The grasses *Diplachne acuminata, Muhlenbergia asperifolia, Spartina patens,* and *Crypsis schoenoides* are halophytes which were first reported from Ontario in 1977 (Catling, Reznicek & Riley, 1977). Catling & McKay (1980) recently made a survey of Na-rich habitats in southern Ontario, listing *Enteromorpha intestinalis, E. prolifera, Najas minor, Poa arida, Suaeda calceoliformis, Spergularia media, Centaurium pulchellum, Solidago sempervirens, Aster subulatus,* and *Pluchea purpurescens* var. *succulenta* for the first time, with records and reference also to *Carex praegracilis, Muhlenbergia asperifolia, Spartina patens, Diplachne acuminata, Juncus compressus, J. gerardii, Spergularia marina, Aster brachyactis,* and others. Thirty species found on Na-enriched soils were also reported, but these belong to the group that are less often confined to Na-rich substrates.

The occurrence of several halophytes disjunct from the Atlantic coast and from the west in the Detroit-Windsor area (Catling & McKay, 1980) make the occurrence of natural salt springs and salt marshes in that area seem especially likely. However, Dr. E. Vandall, historian at the University of Windsor, suggests that the salt-bearing "salina formations vary from 300 to 1500 feet below surface level and these are well covered by other rock formations" and further "the early French in Detroit had to import salt at very high prices" (pers. comm.). A report dated 1788 gave the price of salt in Detroit as 40 shillings a bushel as opposed to 15 shillings in Kingston, and 2 shillings 6 pence in Montreal, which would seem to indicate the lack of a local supply. There is no evidence for salt marshes in Essex Co. areas of Ontario, based on the examination of local history materials, maps and geological reports (R. T. Barlow, Windsor Public Library, pers. comm.). In this area the salt beds are generally about 1000 feet deep, and although water bearing strata occur at 700 feet, they could not pick up any of the salt (R. T. Barlow, pers. comm.). The Canadian Salt Company at Windsor, has confirmed that there are no natural Na springs on their property.

The lack of earlier records of various halophytes now present in southern Ontario and the apparent absence of natural sodium rich habitats very strongly suggests that halophytes are not native.

Pennsylvania

Although Lefond (1969) indicated that the rock salt beds in Pennsylvania are relatively deep (2,200 feet +) and that Pennsylvania has never produced rock salt, there are natural sodium-rich springs in the state. These salt springs are directly related to the salt content of outcropping rocks and connate waters trapped in these rocks (A. R. Geyer, Chief State Geologist, pers. comm.). It is

not surprising that natural brines should occur at the surface in Pennsylvania since they are well documented to the north and west in Ohio and New York. The main areas of Pennsylvania where these springs occur are in the northwest and northeast corners of the state, primarily in Erie and Susquehanna counties.

In the terms of agreement between Thomas Nuttall and Benjamin Smith Barton, Nuttall was to "go down the Ohio to the mouth of the Big Beaver . . . , and thence to the Mahoning Salt Springs on a western branch of the Beaver. These springs will be worth examining for their vegetable and other products. Look for muriatic plants, such as *Salicornia, Glaux, Triglochin,* etc." (Barton, 1810 in Graustein, 1951, p. 78). In his diary of Thursday, April 26, 1810, Nuttall wrote, "In this neighbourhood (Butler) there were also a number of salt licks, but no marine plants about them." Under Friday, April 27, he stated, "I presume that the Mahoning Springs as well as this at Butler are without muriatic plants" (Nuttall, 1810, in Graustein, 1951, pp. 30–31).

It appears that there are no currently active brine wells (A. R. Geyer, pers. comm.) but that in colonial days salt springs and brine wells served as the chief source of salt. The wells were apparently restricted to an area between Erie Co. and Allegheny Co. in the western part of the state.

We are not aware of any western or northern Pennsylvania records for the species listed in table 1 and have not found any reference to the flora of Na-rich substrates (natural or artificial) in the state.

Summary and Discussion

Natural sodium-rich habitats existed in New York, Michigan, Pennsylvania, and Ohio prior to settlement by European man, and in some parts of these states they still exist. In general there is very little information on the natural vegetation associated with these areas. The only endemic described from any of them is *Spergularia alata,* which is poorly understood taxonomically. Definite records of halophytes inland in the northeast prior to the development of a local extractive salt industry include those of *Eleocharis parvula* and *Scirpus olneyi* in Michigan. Native occurrence of other halophytes inland remains a possibility, especially in parts of New York and Ohio.

It appears that between 1850 and 1920, sodium-rich habitats developed rapidly about the numerous salt factories and brine wells in the eastern Great Lakes region. Salt also accumulated about running wells not initially intended to produce brine, and brine sometimes originated from oil wells (e.g., in southwestern Ontario and Ohio—see Pettyjohn, 1971). Halophytes may have been dispersed to these habitats by waterfowl and/or by man on vehicles, in fill, etc.

During the peak of the railway era it appears that many exotic plants were transported in ballast, becoming established where the ballast was dumped many miles from the point of origin. The use of salt to melt ice and facilitate traffic in railway yards created Na-rich substrates. Salt may also have been stockpiled in and near railway yards during the times when it was transported mainly by rail.

With increasing centralization of the salt industry, the tendency for clean-up of the landscape about many industries, the loss of pressure from

aquifers resulting in decline of running wells, and the declining importance of the railway, artificial sodium-rich habitats probably decreased. However, these habitats have recently become more frequent due to the use of de-icing salt (NaCl, 95%; CaCl, 5%). De-icing salt has been used with increasing intensity on eastern North American highways since ca. 1940 (Westing, 1969; Ontario Dept. of Transportation & Communications, pers. comm.). Sodium salts accumulate under certain conditions stressing, and in some cases killing, the non-adapted existing vegetation (Westing, 1966; Hutchinson & Olson, 1967; Davison, 1971; Foster & Maun, 1978). Halophytes are at present spreading into the eastern Great Lakes region from the west and from the eastern seacoast.

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REVIEW

FLOWERING PLANTS: WILLOWS TO MUSTARDS. The Illustrated Flora of Illinois. By Robert H. Mohlenbrock. Southern Illinois University Press, Carbondale, 1980. 286 pp. $18.00.

In this, the eighth volume (second on dicots) of its series, the illustrations for the first time quite consistently catch the spirit of the plants, do not look like they were attempts to resurrect dried specimens, and were evidently drawn and inked at an appropriate scale for the reduction employed. They are excellent.

The keys are quite original, and I found several helpful points when writing up the Michigan mustards a year ago. However, they are very simple keys, usually with only one or two characters in a couplet—not enough to accommodate the range of variation many species display, or to offer much self-correction if one goes astray. And sometimes they simply veer from the facts. For instance, *Matthiola* (the aptly named *M. incana* escapes in Illinois) keys only under "Flowers purplish or reddish" [vs. white] and then under "Plants glabrous"; but the text admits that the flowers may be "even white" and of course the stem and leaves are (as illustrated!) more or less densely pubescent. The single very simple key to *Salix* is based largely on leaves and hence is useless with flowering material of such species as *S. discolor*. Specimens of *S. alba* and *S. fragilis* with (as described in the text) glands at the "upper end" of the petiole will be sidetracked in the very first couplet unless they are forced under "Glands absent at upper end of petiole."

Some valuable hints for identification, beyond the keys, are given in the text, but are not always reliable. *Draba*, for example, is said to be "the only genus of Brassicaceae in the eastern United States with the combination of stellate pubescence and short fruits with several seeds." If this is true, then the author should have merged *Capsella* and *Berteroa* with *Draba*. The petals of *Alyssum alyssoides* are said to be 1.5–2.5 mm long; on all Michigan material I have examined, they are 3–4 mm.

Those who are familiar with the Englerian sequence of families should be warned that this volume does not include "willows to mustards" as covered in manuals by Fernald, Gleason and Cronquist, and many others; it includes only the willow and mustard families (Salicaceae and Brassicaceae) plus the small Tamaricaceae, Capparidaceae, and Resedaceae—117 species in all. The sequence followed is that of Thorne, as explained and listed on pp. 1–3. Names of higher taxa (e.g. orders and families) are grammatically plural, and their usage as singular ["The Salicaceae is . . ."] is "a regrettable barbarism, that should be fought by scientific editors" (Taxon 30: 109. 1981).

References to published literature are sparse. Even the exhaustive 1972 monograph of *Rorippa* by Stuckey is not mentioned (or used). There is no indication at all that many botanists recognize two species of water-cress, even if the author (as do I) prefers not to recognize them at that rank. The epithet of wild radish is consistently misspelled *raphinistrum*. The author calls Balm-of-Gilead *Populus* ✕*gileadensis* but lists in its synonymy the older name *P. candicans;* however his view is that the tree is a hybrid of *P. balsamifera* and *P. deltoides*—for which the older *P.* ✕*jackii* is available. Garlic mustard is called *Alliaria officinalis*, with a note that Patman and Iltis "have given reasons" for calling it *A. petiolata* (in fact they gave no reasons at all, but merely used the older and therefore correct name). It is noted that *Brassica alba* would be correct for white mustard "if" one rejects Gilibert's names, but no explanation is offered for *not* following the Code and rejecting these invalid names; so, too, the horseradish is called *Armoracia lapathifolia* rather than the correct *A. rusticana*.

Botanists in areas adjacent to Illinois will find this volume useful both for identification and for information on range. Michigan readers who know that swamp cottonwood (*Populus heterophylla*) is legally a "threatened species" in our state may be surprised to see that in Illinois it grows only in the southern third—and that its range is not even said to include Michigan (for which published records span more than a century).

—E. G. Voss

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AGE ESTIMATION OF SELECTED
MICHIGAN LARGE TREES

James R. Wells and Paul W. Thompson

Cranbrook Institute of Science
Bloomfield Hills, Mich., 48013

Trees of unusually large size, or age, provide a link with the past and constitute a valuable natural heritage. Locating large trees and tabulating their vital statistics have resulted in a number of publications (Thompson, 1977; American Forestry Association, 1978; McKee, 1979). Other studies have centered on analysis of annual rates of radial growth in every tree in a forested one-hectare plot (Wells, 1978) or selected species distributed over a larger area (Eggler, 1955). Statistical treatment of radial growth has been interpreted by Auclair & Cottam (1973) and Fritts (1958; 1960).

The purpose of this report is to provide data concerning the age of some of the large trees found in Michigan's Lower Peninsula. Our immediate objective has been to sample only one or two trees of a variety of species, but future studies will include many more samples of fewer species. We have used the term "large tree" in order to avoid confusion with previous reports in which "big tree" was used to connote a champion of large size. (However, some of our data were obtained from state champions.) While carrying out our work it became necessary to devise special apparatus for removing the increment borer which sometimes became lodged in the tree. Thus appears a second purpose of this report—to discuss techniques for removing the lodged increment borer.

Critical measurements included height, girth, and crown spread. Height measurements were made with a steel diameter tape calibrated in tenths of a centimeter. For longer measurements we used a Keson fiberglass tape. Increment cores were obtained with a 40 in. (101.6 cm) Finnish-made increment borer. (All the above equipment was obtained from Forestry Suppliers, Inc., 205 W. Rankin St., Box 8397, Jackson, MS, 39204.) Diameter measurements were made at breast height (1.4 m = 4.5 ft. above ground level). Diameters measured with tapes are more accurate than those made with tree calipers if based on a single measurement. This is especially significant in trees having other than a circular cross-sectional shape.

Since the borer weighed 2.4 kg (5.25 lbs) a support was fabricated to aid in starting the coring process. This support (Fig. 1) consisted of a grooved board (3.3 × 3.5 × 50 cm) mounted on a photographic tripod. The drill bit of the increment borer was cradled in the grooved portion of the board. Before drilling the borer was surface-sterilized with 95% ethyl alcohol. The hole was plugged following extraction.

Increment bores were approximately 5 mm in diameter. Length measurements, excluding bark, were obtained immediately after removal from the tree, before changes occurred due to drying. The cores were then surface-sterilized

FIG. 1. Tripod modified as support for increment borer (*upper left*). 2. Increment borer and extractor in position for extracting the drill bit (*upper right*). 3. Detail of extractor's base plate (*lower left*). 4. Increment borer handle (vertical) coupled to extractor (*lower right*).

with 95% ethyl alcohol and stored in stoppered glass tubes. Ring counts were obtained with the aid of a dissecting microscope at 10× magnification.

In diffuse porous wood such as black gum and tulip-tree, a stain helped to delineate annual rings of growth. The staining procedure (Patterson, 1959) consisted of hydrolyzing the cores in a 50% solution of hydrochloric acid for one minute followed by submersion for one minute in ethyl alcohol containing 1% phloroglucin. The result was differential purple staining in the summer wood and less dense spring wood. The tendency for the stain to fade with passage of time minimized over-staining effects. By reducing contact time one can obtain a lighter stain.

In trees with very hard wood, such as hickory, or trees with heartrot, the borer may become lodged during removal of the drill bit. For its removal we tried ropes, block-and-tackle, and a come-along. In order to simplify extraction, a device was fabricated (Fig. 2). The extractor consisted of two joined sections of pipe with a triangular base plate attached to the end. The larger pipe (with five weight-reducing holes) measured 3.8 cm (1.5 in.) in inside diameter and 40.6 (16 in.) in length. A nut (machined to fit the pipe's inside diameter) was inserted into the distal end of the larger pipe and secured by three radially arranged metal dowell pins. The smaller pipe was a 30 cm (12 in.) length of continuously threaded pipe (19 mm = 0.75 in. inside diameter) with threads matching those of the nut. It was threaded through the nut mounted in the end of the larger pipe. The continuously threaded pipe was secured to the triangular base plate with a nut on each side. Three eye-bolts (Fig. 3), threaded into the base plate, could be adjusted to fit the ridges and fissures of the bark. The bolts (diameter 0.375 in. = 9.5 mm) hold the plate tangential to the borer and prevent the base plate from rotating during borer removal. In Fig. 4 is shown the slot in the end of the larger pipe into which is seated the mid-section of the borer handle. By turning the handle of the borer counterclockwise, the two coupled pipes gradually become longer as a unit. This process exerts a steady and continuous extracting force on the lodged borer.

A number of sources of error occur during the process of age estimation of trees. Growth rates, even in the same species, vary considerably according to climatic regime and genetic variability. Also, differential growth rates can be expected in the same tree as it proceeds from youth to maturity. For example, a young tree beneath a forest canopy may grow at a slower rate than when its crown reaches canopy height where more light exists. Other factors which may cause variation include differences in habitat caused by clearing, samples taken on the south side of the tree versus the north side, unusual habitats such as roadsides or lawns and location of the tree within the geographic range of the species. Owing to these factors it is most useful to obtain increment core lengths equal to the entire radius of the tree's wood (exclusive of bark). We made efforts to bore at least to the center of the tree but were not always successful owing to the extreme resistance of hard wood. In several trees the rotted heart wood precluded taking a full radial length core. We therefore had to estimate the number of annual growth rings by the following formula:

Table 1. Tree measurements and estimated age of selected Michigan large trees.*

Species	Collection Number	County	Height	Crown Spread	Girth	Diameter	Radius	Increment Core Length	Core Length Counted	No. Rings Counted	Estimated Age
Acer negundo (box elder)	39	Washtenaw	101 (30.8)	110 (33.5)	205.5 (521.9)	65.4 (166.2)	32.7 (83.1)	15.0 (38.0)	10.5 (26.6)	70	218
Acer saccharinum (silver maple)	32	Oakland	125 (38.1)	134 (40.8)	279.7 (710.3)	89.1 (226.2)	44.6 (113.1)	14.6 (37.0)	14.6 (37.0)	98	300
Acer saccharum (sugar maple)	16	Oakland	106 (32.3)	63 (19.2)	91.5 (232.4)	29.1 (74.0)	14.6 (37.0)	14.6 (37.0)	12.5 (31.7)	154	180
Acer saccharum (sugar maple)	24	Oakland	88 (26.8)	75 (22.9)	98.3 (249.6)	31.3 (79.5)	15.7 (39.8)	15.2 (38.5)	13.3 (33.7)	152	179
Acer rubrum (red maple)	13	Oakland	116 (35.4)	52 (15.9)	86.0 (218.4)	27.4 (69.6)	13.7 (34.8)	15.6 (39.5)	11.8 (30.0)	78	91
Carya cordiformis (bitternut hickory)	18	Oakland	108 (32.9)	48 (14.6)	65.9 (167.4)	21.0 (53.3)	10.5 (26.7)	11.0 (28.0)	9.3 (23.5)	130	147
Carya glabra (pignut hickory)	1	Oakland	115 (35.1)	59 (18.0)	82.0 (208.3)	26.1 (66.3)	13.1 (33.3)	8.3 (21.1)	8.3 (21.1)	125	197
Carya ovata (shagbark hickory)	15	Oakland	86 (26.2)	67 (20.4)	76.0 (193.1)	24.2 (61.5)	12.1 (30.8)	12.6 (32.0)	11.4 (29.0)	102	108
Castanea dentata (American chestnut)	3	Newaygo	54 (16.5)	67 (20.4)	107.1 (271.8)	34.1 (86.6)	17.1 (43.4)	18.3 (46.5)	11.9 (30.2)	88	126
Catalpa bignonioides (southern catalpa)	42	Lenawee	91 (27.7)	82 (25.0)	151.2 (384.0)	48.2 (122.3)	24.1 (61.2)	8.2 (20.9)	8.2 (20.9)	64	187
Fagus grandifolia (beech)	22	Oakland	73 (22.3)	59 (18.0)	75.8 (192.5)	24.1 (61.3)	12.1 (30.7)	11.5 (29.2)	8.7 (22.0)	80	111
Fagus grandifolia (beech)	26	Berrien	99 (33.2)	66 (20.1)	78.5 (199.4)	25.0 (63.5)	12.5 (31.8)	7.7 (19.5)	5.0 (12.6)	78	195
Fraxinus americana (white ash)	21	Oakland	98 (29.9)	69 (21.0)	118.9 (302.1)	37.9 (96.2)	18.9 (48.1)	18.2 (46.1)	13.4 (33.9)	75	106
Fraxinus americana (white ash)	43	Lenawee	99 (30.2)	101 (30.8)	247.4 (628.3)	78.8 (200.1)	39.4 (100.1)	11.9 (30.2)	9.3 (23.5)	43	182
Juglans nigra (black walnut)	36	Oakland	119 (36.3)	116 (35.4)	227.2 (577.1)	72.4 (183.8)	36.2 (91.9)	13.2 (33.5)	13.2 (33.5)	103	283
Larix decidua (European larch)	40	Lenawee	72 (22.0)	68 (20.7)	106.5 (270.4)	33.9 (86.1)	17.0 (43.1)	13.0 (33.0)	13.0 (33.0)	109	143

Species	No.	County									
Liriodendron tulipifera (tulip-tree)	28	Berrien	119 (36.3)	47 (14.3)	65.7 (166.7)	20.9 (53.1)	10.5 (26.6)	11.0 (28.0)	9.9 (25.2)	69	73
Liriodendron tulipifera (tulip-tree)	38	Wayne	101 (30.8)	88 (26.8)	170.2 (432.4)	54.2 (137.7)	27.1 (68.9)	14.0 (35.5)	11.9 (30.3)	78	178
Nyssa sylvatica (black gum)	29	Berrien	71 (21.6)	28 (8.5)	49.3 (125.0)	15.7 (39.8)	7.9 (19.9)	7.8 (19.8)	3.5 (9.0)	36	81
Nyssa sylvatica (black gum)	35	Macomb	77 (23.5)	56 (17.1)	104.2 (264.7)	33.2 (84.3)	16.6 (42.2)	7.7 (19.6)	7.7 (19.6)	93	200
Ostrya virginiana (hop hornbeam)	23	Oakland	63 (19.2)	47 (14.3)	42.2 (107.1)	13.4 (34.1)	6.7 (17.1)	6.8 (21.4)	6.5 (16.4)	215	222
Picea abies (Norway spruce)	31	Oakland	83 (25.3)	78 (23.8)	139.5 (354.2)	44.4 (112.8)	22.2 (56.4)	4.2 (10.6)	4.2 (10.6)	29	154
Pinus banksiana (jack pine)	9	Roscommon	70 (21.3)	21 (6.4)	26.1 (66.3)	12.2 (31.0)	6.1 (15.5)	7.6 (19.2)	4.1 (10.5)	62	92
Pinus banksiana (jack pine)	10	Roscommon	65 (19.8)	20 (6.1)	54.0 (137.2)	17.2 (43.7)	8.6 (21.9)	9.3 (23.5)	9.3 (23.5)	69	91
Pinus resinosa (red pine)	5	Roscommon	105 (32.0)	46 (14.0)	94.3 (239.6)	30.0 (76.3)	15.0 (38.2)	17.0 (43.2)	12.2 (31.0)	201	247
Pinus resinosa (red pine)	6	Roscommon	97 (29.6)	48 (14.6)	96.5 (245.1)	30.7 (78.0)	15.4 (39.1)	17.3 (43.9)	12.6 (32.0)	185	226
Pinus resinosa (red pine)	11	Crawford	98 (29.9)	43 (13.1)	87.9 (223.5)	28.0 (71.1)	14.0 (35.6)	13.8 (35.1)	11.3 (28.7)	151	187
Pinus resinosa (red pine)	12	Crawford	97 (29.6)	38 (11.6)	87.0 (221.0)	27.7 (70.4)	13.9 (35.3)	15.0 (38.1)	11.7 (29.8)	150	178
Pinus strobus (white pine)	7	Roscommon	106 (32.3)	56 (17.1)	109.3 (277.6)	34.8 (88.4)	17.4 (44.2)	21.0 (53.3)	14.2 (36.0)	103	126
Pinus strobus (white pine)	8	Roscommon	116 (35.4)	45 (13.7)	112.1 (284.5)	35.7 (90.6)	17.8 (45.3)	13.4 (34.0)	13.3 (33.8)	68	91
Populus deltoides (cottonwood)	41	Lenawee	118 (36.0)	109 (33.2)	221.7 (563.0)	70.6 (179.3)	35.3 (89.7)	19.9 (50.5)	19.9 (50.5)	108	192
Quercus alba (white oak)	4	Oakland	120 (36.6)	79 (24.1)	134.9 (337.2)	43.1 (107.7)	21.6 (53.9)	15.8 (39.4)	13.6 (34.0)	90	143
Quercus alba (white oak)	14	Oakland	128 (39.0)	72 (22.0)	126.2 (320.3)	40.2 (102.0)	20.1 (51.1)	11.8 (30.0)	10.1 (25.7)	163	324
Quercus macrocarpa (bur oak)	19	Oakland	102 (31.1)	66 (20.1)	115.6 (293.6)	36.8 (93.5)	18.4 (46.8)	19.8 (50.2)	17.3 (44.0)	215	229
Quercus muhlenbergii (chestnut oak)	20	Oakland	110 (33.5)	63 (19.2)	92.0 (233.6)	29.3 (74.4)	14.7 (37.2)	12.9 (32.7)	12.8 (32.6)	154	177

Table 1. Continued

Species	Collection Number	County	Height	Crown Spread	Girth	Diameter	Radius	Increment Core Length	Core Length Counted	No. Rings Counted	Estimated Age
Quercus palustris (pin oak)	37	Wayne	106 (32.3)	84 (25.6)	147.1 (373.7)	46.9 (119.0)	23.5 (59.5)	11.0 (27.9)	8.9 (22.6)	42	111
Quercus ×*schuettei* (= bur oak × swamp white oak) (*Q. macrocarpa* × *Q. bicolor*)	34	Oakland	122 (37.2)	134 (40.8)	227.8 (578.7)	72.6 (184.3)	36.3 (92.2)	12.8 (32.5)	12.8 (32.5)	60	170
Salix babylonica (weeping willow)	30	Oakland	92 (28.0)	93 (28.4)	209.1 (531.0)	66.6 (169.1)	33.3 (84.6)	15.4 (39.0)	13.2 (33.6)	96	242
Tilia americana (basswood)	17	Oakland	90 (27.4)	49 (14.9)	110.3 (280.1)	35.1 (89.2)	17.6 (44.6)	7.2 (18.2)	7.2 (18.2)	105	257
Tsuga canadensis (hemlock)	25	Berrien	109 (33.2)	42 (12.8)	70.5 (179.0)	22.4 (57.0)	11.2 (28.5)	11.7 (29.6)	7.6 (19.3)	146	215
Tsuga canadensis (hemlock)	27	Berrien	110 (33.5)	44 (13.4)	69.1 (175.2)	22.0 (55.8)	11.0 (27.9)	10.6 (27.0)	9.3 (23.5)	139	164
Ulmus pumila (Siberian elm)	33	Oakland	120 (36.6)	147 (44.8)	163.6 (415.1)	52.1 (132.2)	26.0 (66.1)	16.7 (42.3)	16.7 (42.3)	38	59

*Tree height and spread are listed in feet (meters), other measurements are inches (cm); girth measurements taken at 4½ ft. above ground; (1″ = 2.54 cm; 1 ft. = 0.3048 m).

$$\text{estimated age} = \frac{(\text{number of rings counted} \times \text{radial length})}{\text{length of core segment counted}}$$

If for any reason a portion of the total core length could not be counted that length was excluded from measurements shown in the Table 1 column headed "core length counted." An estimate of the number of rings in the theoretical length could then be extrapolated using the preceding formula. Increment cores, if not taken on a radial axis, will be tangential to that axis and the proportionate length of each growth ring will be greater than if measured radially. The result is that trees will appear younger than their true age if estimates are extrapolated.

Since Table 1 concerns only 43 trees, and less than 50% of Michigan's tree species, any suggestion that our data supports a statistically significant correlation between size and age should be avoided. All tree samples were taken during 1979. Collection numbers reflect chronology of sampling. Numbers 32, 39 and 43 represent national champions; numbers 33, 34, and 36 are state champions. Although the purpose of Table 1 is to present some idea of possible sizes and ages of some of our largest trees in Michigan's Lower Peninsula, we found that many extremely large trees had rotted wood which necessitated extrapolation of their ages. We found only two trees (nos. 14 and 32) as old as 300 years. A few very large trees were less than 100 years in age. The Siberian elm, a national champion, was only 59 years old. The average for all our samples was 167 years. We have heard of unpublished estimates of ages on the order of 500 to 600 years for large pines in the Upper Peninsula. It would be interesting to verify these as candidates for Michigan's oldest trees.

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PUBLICATIONS OF INTEREST

THE VEGETATION AND PHYTOGEOGRAPHY OF COASTAL SOUTHWESTERN JAMES BAY. By J. L. Riley & S. M. McKay. Royal Ontario Museum Life Sciences Contributions 124. 1980. 81 pp. $5.50. The first third of this publication describes the major coastal and estuarine communities of vascular plants studied just north of the mouth of the Moose River, with a floristic analysis stressing disjunctions. A checklist provides habitat and locality details for nearly 400 species in the study areas, and maps show for 52 species the "northeastern North American distribution." In fact, the maps (like those by most Canadian botanists) show definite localities only for the Canadian portion of the area—admittedly the most interesting under the circumstances; range to the south (and often east and west of the Hudson Bay—Lake Superior region) is merely outlined. Nine photographs show good habitat views.

GUIDE TO THE VASCULAR PLANTS AND WILDLIFE OF THE ROUGE RIVER VALLEY in Metropolitan Toronto and Durham Region. By John L. Riley. Ontario Field Biologist Special Publication 1. 1978. 54 pp. $1.50. Includes an annotated list, with common and scientific names, of 626 taxa of vascular plants collected in a 625-hectare ravine complex on the edge of metropolitan Toronto. The introduction describes five basic habitats, with maps and aerial photos. There are brief notes on wildlife. A model publication of its kind, available from the Toronto Field Naturalists' Club, 49 Craighurst Ave., Toronto, Ontario, Canada M4R 1J9.

PODS WILDFLOWERS AND WEEDS IN THEIR FINAL BEAUTY Great Lakes Region, Northeastern United States and Adjacent Canada. By Jane Embertson. Scribner's, New York, 1979. 186 pp. $14.95. This is an attractively designed book, the basic format including a small color photo of a species in bloom in its natural habitat, associated with a somewhat closer view of it in fruiting condition. Often pictured is also an arrangement in vase or bowl. Short notes give identification aids and remarks. The idea, except that the pictures are in color, is quite reminiscent of the Michigan Botanical Club's "Winter Wildflowers" (which, incidentally, is nowhere mentioned)—especially the dust jacket illustration (compared to our cover). The worst feature of the book is the incredibly inept title and persistent misuse of the word "pod" to refer to *any* fruit (and even more), in the face of universal definition that restricts "pod" to a fruit that splits open naturally when ripe. The author defines pod as "any container or vessel holding seeds"—"for want of a better word." A better (i.e. accurate) word for what is uniquely defined as a pod is simply "fruit"! Furthermore, the author does not follow her own definition, as when she describes nodding thistle as having pods that "'nod' down" (when it is the whole head of fruits that nods) and purple loosestrife as having "upright seeds" that "encircle the spikes in whorls" (when in fact it is the "pods" that are upright). And further fuzzy thinking produces meaningless phrases like "fuzzy-headed pods" for goldenrod. The dust jacket claims that the photographer worked closely with the author "to make sure each pod was photographed in its most natural surrounding and was easy to identify." In fact, there is no evidence that *any* "pod" in the entire book was photographed in its natural surrounding; all appear against a uniform (usually "black velvet") background. For pictures of dry fruiting plants, and some ideas on arrangements, the book is worth owning—if you can endure a suffering twinge whenever the word "pod" is mis- and over-used.

NORTH AMERICAN FLORA Series II Part 10. Compositae. New York Botanical Garden, 1978. 245 pp. $20.00. This substantial number of its series covers three tribes of Compositae: Mutisieae, Senecioneae, and Vernonieae, by a total of 12 authors. The largest treatment is that of *Senecio* (105 recognized species) by T. M. Barkley; among the other genera familiar in our area are *Cacalia* by R. W. Pippen, *Petasites* by A. Cronquist, and *Vernonia* by S. B. Jones and W. Z. Faust. Keys, full descriptions, and synonymy are provided, but there are no illustrations or maps—only references to some published illustrations and brief statements of distribution.

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A GEMMIPAROUS POPULATION OF
MARCHANTIA POLYMORPHA VAR. AQUATICA
IN CHEBOYGAN COUNTY, MICHIGAN

Raymond H. Hollensen

Dept. of Natural Science,
Michigan State University, East Lansing, 48824

Jane Taylor

Dept. of Biology,
University of Michigan—Flint, Flint, 48503

The earliest authenticated specimens of *Marchantia polymorpha* var. *aquatica* from Cheboygan County, Michigan, were collected by Margaret Fulford in 1951 at Iron Bridge, Carp Creek (UMBS). Campbell (1969), in her account of *Marchantia* in Michigan, gave further documentation of the Iron Bridge population, and we have had the locality under observation for an extended period of time (1968—1981) in order to determine the seasonal events enabling this colony to persist.

In July and August the thalli are usually abundant in log-bounded pools, suspended in water and often mingled with the leafy liverwort, *Chiloscyphus.* One such pool, bounded by logs of *Thuja occidentalis,* has been repopulated by the aquatic *Marchantia* for 13 years. This suggests that this particular area is not subject to flooding and subsequent erosion, although there is a seasonal change in water level. From August through November the water level tends to drop. During the winter the pools are frozen, covered with snow, and subjected to air temperatures often below minus 18°C. With melting of snow and ice in April, there is a rise and fall of the water level (rarely exceeding two decimeters) causing some of the thalli which originally were suspended in the pools to be stranded above the water level upon decaying logs. New growth of the stranded thalli begins in the spring at the time of, or shortly before the flowering of *Caltha palustris.* By midsummer, these thalli are usually dried up and overgrown by other bryophytes.

Gemma cup production regularly occurs on new growth on the stranded thalli. The cups are initiated along the midline of the thallus immediately behind the apical notch. Due to continued growth of the apex of the thallus, the mature cup is located 8—10 mm behind the tip of the thallus. New growth of thallus tips and gemma cups occurs in a similar manner on the thalli of suspended plants at the same time. Gemma cup production on the suspended thalli has been rare in some years and prolific in other years.

The photomicrograph (Fig. 1) of a paraffin embedded, microtomed, longitudinally sectioned, and stained portion of a gemmiparous, suspended thallus shows several unique features. The outer portion of the wall of the gemma cup has small air chambers (a) which lack photosynthetic filaments. There are small
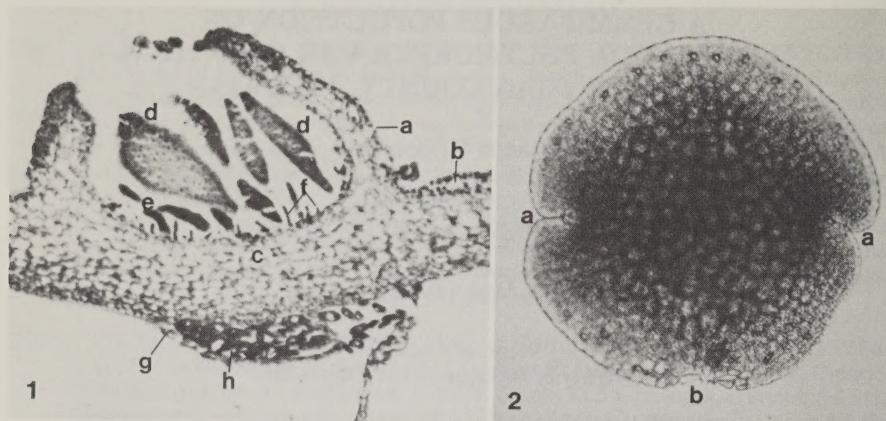
Fig. 1. Gemma cup and thallus of *Marchantia polymorpha* var. *aquatica,* l.s., X75. a, air chamber in wall; b, air chamber in thallus; c, thallus ventral to cup; d, mature gemmae; e, immature gemmae; f, slime papillae; g, ventral scale, h, rhizoid cluster. Fig. 2. Mature, living gemma of *Marchantia polymorpha* var. *aquatica,* X200. a, apical notches; b, stalk scar.

air chambers (b) in the dorsal portion of the thallus antical to the cup. It is this region of the otherwise suspended thallus which is at the surface of the water. The cells of the thallus (c) ventral to the cup, are relatively large and parenchymatous, with no development of air chambers. The gemma cup, though less well developed than in the terrestrial variety, contains mature, discoid gemmae (d), immature discoid gemmae (e), and slime papillae (f). The peculiar shapes of the various gemmae (d) are due to their oblique angles to the plane of sectioning. A photograph of a living gemma in surface view is shown in Fig. 2. Each gemma is attached by a one-celled stalk to the bottom of the gemma-cup. When the gemma is mature, the stalk breaks off, leaving a scar (Fig. 2b). It should be noted that there are two apical notches (Fig. 2a) on each gemma. Since each notch gives rise to a new plant, the reproductive potential is actually twice the number of gemmae. Gemma cups produced on suspended thalli tend to be less well developed than on stranded thalli. As in the terrestrial variety and in the stranded thalli, both the ventral scale (Fig. 1g) and rhizoid cluster (h) are present.

The gemmae, up to 360 per cup, are easily dislodged by raindrops. One drop falling into the conical cup will flip nearly all mature gemmae out simultaneously. Those gemmae which do not fall into the pools or into the stream fall into a continuous mat of bryophyte vegetation and are unable to compete. Many of the gemmae which fall into the water immediately float. These floating gemmae have tiny bubbles tightly adhering to them and if flipped into pools may contribute to the population in those pools. Floating gemmae flipped into the stream may be trapped in pools downstream, and establish new colonies.

Those which immediately sink begin to photosynthesize, slowly rise, and eventually float.

These mechanisms maintain the populations in the pools, adding new plants produced from gemmae to the continuing growth of older thalli from the preceding year. Both suspended new and old thalli in the pools continue to grow through the spring and into the summer. These aspects account for the persistent population in the pools and also for downstream distribution. By late spring gemma production has ceased. It would appear that *Marchantia polymorpha* var. *aquatica* at Iron Bridge is an excellent example of asexual propagules playing a key role in the persistence of a liverwort population.

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REVIEW

GRASSES OF ONTARIO. By William G. Dore & J. McNeill. Agriculture Canada Monograph 26. 1980. 566 pp. $12.00 (Canada); $14.40 (other countries, Canadian funds).

This long-awaited volume is a substantial hardcover book which will be useful to botanists over a wide area, especially in and adjacent to Ontario. Among the illustrations are many photographs of florets, spikelets, and grains—not single ones but large variable samples. Distribution maps (262) show known Ontario and sometimes adjacent Canadian localities, but these often do not include collections made during the past 15—20 years, and there are sometimes minor discrepancies between the maps and the text. Maps 181 and 182 are transposed. The sequence of genera is the familiar Englerian one employed in most local manuals, but there is no mention of subfamilies or tribes, and there is a single key to genera. The keys look original and workable, although one can always search out problems; since *Muhlenbergia uniflora*, for example, often has two florets per spikelet, it will not always key to genus. Full descriptions of the species are not given, but stress in the text is placed on helpful diagnostic and field characters. The nomenclature is very up to date and so is the useful list of references. There is said to be a record of *Calamagrostis pickeringii* from Isle Royale, but this was referred to *C. lacustris* in *Michigan Flora* (p. 198). Naturalists in the entire Great Lakes region will welcome this attractive, uniquely well illustrated, practical, and accurate manual, which is available from the Canadian Government Publishing Centre, Hull, Quebec, Canada K1A 0S9 (checks payable to Receiver General of Canada).

—E. G. Voss

The May issue (Vol. 20, no. 3) was mailed May 27, 1981.

CONTENTS

On the cover: *American Lotus,*
a rare and endangered species, in Monroe
County, Michigan, August 9, 1980.
Photo by Clayton Alway